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The ecological effects of urbanization of coastal watersheds: historical increases in nitrogen loads and eutrophication of Waquoit Bay estuaries

Jennifer L. Bowen and Ivan Valiela

Abstract: Historical changes in land use on coastal watersheds have increased rates of land-derived nitrogen loading to estuaries and altered their biogeochemistry and food webs. We used information on human populations and land uses within the watershed of Waquoit Bay, Cape Cod, Massachusetts, U.S.A., to model how nitrogen loads derived from atmospheric deposition, fertilizer use, and wastewater disposal have changed since the 1930s. Nitrogen loading into Waquoit Bay more than doubled between 1938 and 1990. The predominant source of nitrogen added to the bay changed from atmospheric deposition to wastewater disposal during the 1980s, reflecting the increasing urbanization of Cape Cod. Larger nitrogen loads increased nitrogen concentrations in the water, altering the assemblage of primary producers and resulting in eutrophication of the estuary. Biomass of phytoplankton and macroalgae increased, and areal cover of eelgrass (*Zostera marina*) decreased, with increasing nitrogen load. An increase in nitrogen load from 15 to 30 kg N·ha^{-1}·year^{-1} virtually eliminated eelgrass meadows. Land-use changes prompted by urban sprawl can therefore be linked to marked changes in water quality and eutrophication of receiving waters.

Résumé : Les changements historiques d'utilisation des terres dans les bassins versants côtiers ont augmenté les taux de charge de l'azote d'origine terrestre dans les estuaires et y ont modifié la biogéochimie et les réseaux alimentaires. Des données sur les populations humaines et l'utilisation des terres dans le bassin versant de la baie de Waquoit du cap Cod au Massachussetts, États-Unis, ont permis de modéliser comment les charges d'azote reçues par précipitation atmosphérique, les engrais et les eaux de rejet ont changé depuis les années 1930. La charge d'azote à la baie de Waquoit a plus que doublé entre 1938 et 1990. Durant les années 1980, la source principale d'azote dans la baie est passée de la précipitation atmosphérique d'azote à l'azote des eaux de rejet, un reflet de l'urbanisation croissante du cap Cod. Les charges accrues d'azote ont augmenté les concentrations d'azote dans l'eau, ce qui a modifié la composition des producteurs primaires et résulté en l'eutrophisation de l'estuaire. Les biomasses du phytoplancton et des macroalgues ont augmenté avec l'apport plus important d'azote, alors que la surface couverte par la zostère (*Zostera marina*) a diminué. Les charges accrues d'azote de 15–30 kg N·ha^{-1}·année^{-1} ont presque complètement éliminé les marais à zostères. Les changements dans l'utilisation des terres consécutifs à l'étalement urbain peuvent donc être reliés à des modifications marquées de la qualité de l'eau et à l'eutrophisation des eaux réceptrices.

[Traduit par la Rédaction]

Introduction

Enrichment of coastal waters from land-derived nitrogen is one of the most pervasive threats to aquatic ecosystems today (Carpenter et al. 1998). Human-induced alterations to coastal watersheds have invariably resulted in changes in the ecology of aquatic systems. Nitrogen typically limits the growth of estuarine producers (Ryther and Dunstan 1971; Howarth 1988) and increases in the supply of nitrogen induce eutrophication in coastal waters (Nixon 1995).

In a large geographical context, all available nitrogen is derived from atmospheric sources through N_2 fixation. Nitrogen in fertilizers is fixed from N_2 gas and is then applied to major crops. The food we ingest transforms the nitrogen derived from fertilizer into nitrogen that is released as wastewater. On a watershed scale it is helpful to separate nitrogen delivery into three components: atmospheric deposition both within and outside the watershed, fertilizer application on lawns, turf, and agriculture, and disposal in human-derived wastewater (Lee and Olsen 1985; Cole et al. 1993). Some portion of the nitrogen that is deposited on watersheds from these sources is then delivered from land to coastal systems (Hinga et al. 1991; Correll et al. 1992).

Numerous mechanistic and empirical models have been developed to predict both the amount of land-derived nitrogen entering surface water and groundwater and the ecological effects of that nitrogen on the receiving water body. These range from relatively simple models based on human population densities within watersheds (Cole et al. 1993) to more complex models that include terms for atmospheric inputs and land-use classifications (Valiela et al. 1997*a*). We used one such model to reconstruct changes in nitrogen loading to the estuarine complex in Waquoit Bay, Cape Cod, Massachusetts, U.S.A. (Fig. 1).

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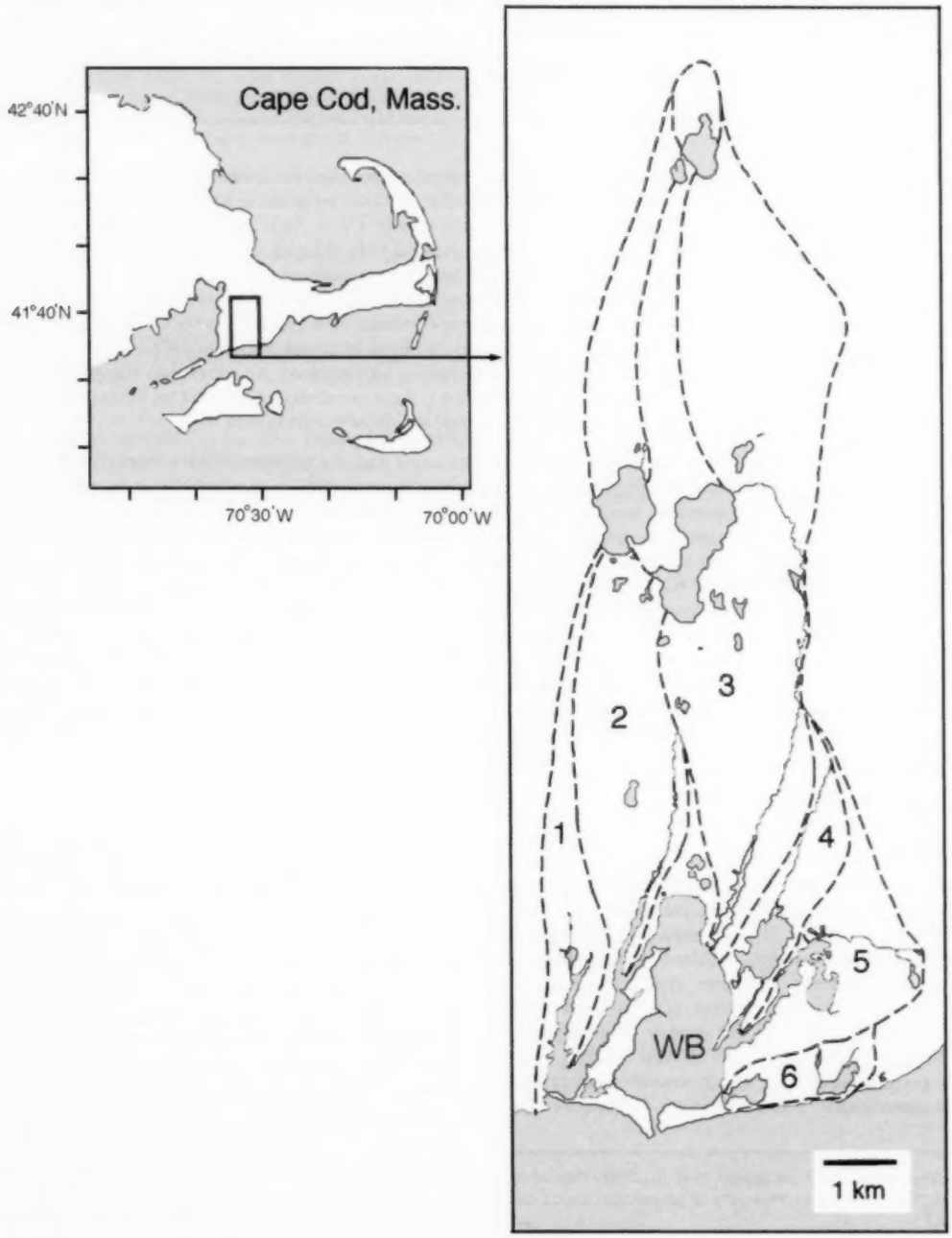
Fig. 1. Location of Waquoit Bay (WB), Cape Cod, Massachusetts, U.S.A., and its subwatersheds (1–6). Subwatersheds were delineated using a MODFLOW groundwater transport model by J. Brawley and C.-H. Sham, and are reported along with measured nitrogen loads in Valiela et al. (2000*a*). Nitrogen loads for each subwatershed are as follows: (1) Eel River, 93 kg·ha^{-1}·year^{-1}; (2) Childs River, 601 kg·ha^{-1}·year^{-1}; (3) Quashnet River, 403 kg·ha^{-1}·year^{-1}; (4) Hamblin Pond, 15 kg·ha^{-1}·year^{-1}; (5) Jehu Pond, 16 kg·ha^{-1}·year^{-1}; (6) Sage Lot Pond, 12 kg·ha^{-1}·year^{-1}.



The pattern of changing land use in the Waquoit Bay watershed is representative of regional trends. Agricultural land in the northeastern U.S.A. has decreased from 4.6 million ha of major crops in New England and New York in 1910 to only 1.5 million ha in 1995. In the same region livestock decreased from 3.2 million head to just over 2 million head during the same time period (U.S. Department of Agriculture (USDA) 1993, 1999).

Despite the decrease in agricultural area, the pressing need to increase crop yields and the rise in industrial manu-

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facturing of synthetic fertilizers since the 1940s have fostered an increase in agriculturally derived nitrogen loading to most U.S. waters. In recent decades, fertilizer has accounted for up to 60% of net nitrogen inputs to land in the U.S.A. (Jordan and Weller 1996). Nitrogen from fertilizers accounts for only 19% of the total nitrogen inputs to the northeastern U.S.A., but the net import of food and livestock feed accounts for another 32% of nitrogen inputs to the region (Jordan and Weller 1996). This importation, another consequence of the decrease in agricultural land, converts nitrogen from synthetic fertilizers that are produced outside the region to nitrogen in wastewater that is deposited locally. Since 99% of ingested nitrogen is excreted (Smil 1999), nearly 420 million kg N·year^{-1} is imported into the watersheds of the northeastern U.S.A.

There has been reforestation of some of the agricultural land in the New England area (Foster 1992), but much of the land has given way to urban expansion, particularly in coastal regions. The populations of coastal counties in the U.S.A. are increasing three times faster than the U.S. population as a whole (Culliton et al. 1989). Over the last 60 years the population of Cape Cod has exceeded even that rate, increasing by a factor of nearly 5, from 32 000 in 1930 to over 180 000 in 1990 (www.census.gov). As a result of the changes in land use and agricultural practices, substantial changes have occurred in the amount of nitrogen from human NO_x emissions (Holland et al. 1999), fertilizers (Smil 1997), and wastewater both in the northeastern U.S.A. and on Cape Cod. Changes in nitrogen loading and the resultant alterations in estuarine ecology in Waquoit Bay might mirror, as a microcosm, changes that have occurred throughout the northeastern U.S.A.

In this paper we use land-cover data and reconstructed rates of atmospheric deposition and fertilizer use to develop regional changes in the quantity of nitrogen from the three major sources to Waquoit Bay during the last two-thirds of the 20th century. We also demonstrate that the changes in nitrogen loads from the Waquoit Bay watershed were sufficient to alter the ecology of the estuaries by assessing the effects of urbanization on ecological indicators, including phytoplankton, macroalgae, seagrasses, and scallops. The reconstruction that we present in this paper defines, within the limits of available data, how the nitrogen load into Waquoit Bay has changed since 1938. Long-term monitoring of nutrient inputs to most coastal systems is rare, and historical records of primary production are difficult to find. The reconstruction of land use and resultant nitrogen loads into Waquoit Bay offer the opportunity to understand that temporal setting.

Methods

To recreate historical nitrogen loads we needed a model that was complex enough to incorporate changes in each source of nitrogen, but that was not so complex that it required arcane data which would be impossible to recreate from scant historical records. We applied a previously developed (Valiela et al. 1997*a*) and field-verified (Valiela et al. 2000*a*) nitrogen-loading model (NLM) to reconstruct the changes in nitrogen loading to Waquoit Bay since the 1930s.

The Waquoit Bay NLM (Fig. 2) predicts nitrogen inputs to watersheds from atmospheric deposition, fertilizer use, and wastewater disposal, and then calculates the groundwater-delivered nitrogen loads into estuaries (Valiela et al. 1997*a*, 2000*a*). NLM was derived from literature reviews and research in the Waquoit Bay estuarine system. It includes terms for each of the major sources of nitrogen and applies each of these sources to the different land uses in the watershed, tracking the losses and transformations that occur as the nitrogen moves through the landscape (Fig. 2). One example of how NLM works is that 65% of nitrogen from atmospheric sources deposited on forests is lost as it travels through forest biomass and soils, 61% of the remaining nitrogen is lost in the vadose zone, and then 35% of the surviving nitrogen is lost in the aquifer before the remainder reaches the Bay at the seepage face (Valiela et al. 1997*a*, 2000*a*).

We have compared the structure and performance of NLM and six other published loading models (I. Valiela, J.L. Bowen, and K.D. Kroeger, unpublished data). In terms of model structure, NLM is among the most inclusive of transformation and transport terms. Its structure (Fig. 1) mirrors the path and fate of nitrogen moving through watersheds in a biogeochemically comprehensive fashion. In terms of performance, the predictions of nitrogen loads from watersheds made by NLM are statistically indistinguishable from measured nitrogen loads (Valiela et al. 2000*a*); the other models made predictions that required post-hoc correction terms of 26–76% to accurately match measured values (I. Valiela, J.L. Bowen, and K.D. Kroeger, unpublished data).

Using NLM to calculate historical nitrogen loads required that we compile data on changes in the land-use mosaic of the Waquoit Bay watershed, as well as on historical trends in atmospheric deposition, fertilizer use, and wastewater disposal, the three major sources of nitrogen. Below we address how each of these was estimated.

Changes in the land-use mosaic

To model nitrogen loads into receiving estuaries, NLM requires inputs of the areal extent of major land covers within the adjoining watershed. The land uses in the Waquoit Bay watershed include areas of natural vegetation, freshwater ponds and wetlands, agricultural land, cranberry bogs, impervious surfaces (including roads, roofs, driveways), lawns and other turf, and houses (Fig. 2). Aerial photographs taken in 1938, 1944, 1951, 1955, 1971, 1980, 1985, and 1990 were incorporated into ArcInfo and analyzed to determine the areal cover represented by each type of land use (Brawley et al. 2000).

Changes in nitrogen sources

Atmospheric deposition

To estimate amounts of nitrogen deposited from the atmosphere during the period of study we used a historical reconstruction of nitrogen deposition to the northeastern region of the U.S.A. and the Maritime Provinces of Canada (Bowen and Valiela 2001). We compiled historical data on wet nitrogen deposition from 1910 to the present from extensive literature reviews. Historical data on the proportions of dry deposition and deposition of dissolved organic nitrogen (DON) do not exist in the literature, so we applied constant adjustment factors to the wet-deposition time course to estimate deposition of total nitrogen over the course of the century.

We estimated dry deposition and deposition of DON as follows. A dry deposition adjustment factor was developed using data from the National Dry Deposition Network and the Integrated Forest Studies Program. These data indicate that oxidized forms of dry nitrogen deposition were between 25 and 70% of oxidized wet deposition, and reduced forms were between 2 and 33% of wet NH_4-N deposition (Lovett and Lindberg 1993). In our calculation we used 48%, the mean of these ranges, as a dry-deposition factor for oxidized nitrogen and 18% as a dry-deposition factor for reduced forms of nitrogen (Bowen and Valiela 2001). Organic nitrogen ranged from 11 to 90% of total deposited nitrogen in different areas of the world (Timperley et al. 1985). We used an organic nitrogen adjustment factor of 52% of the total nitrogen deposition based on local measurements (Valiela et al. 1978) to account for

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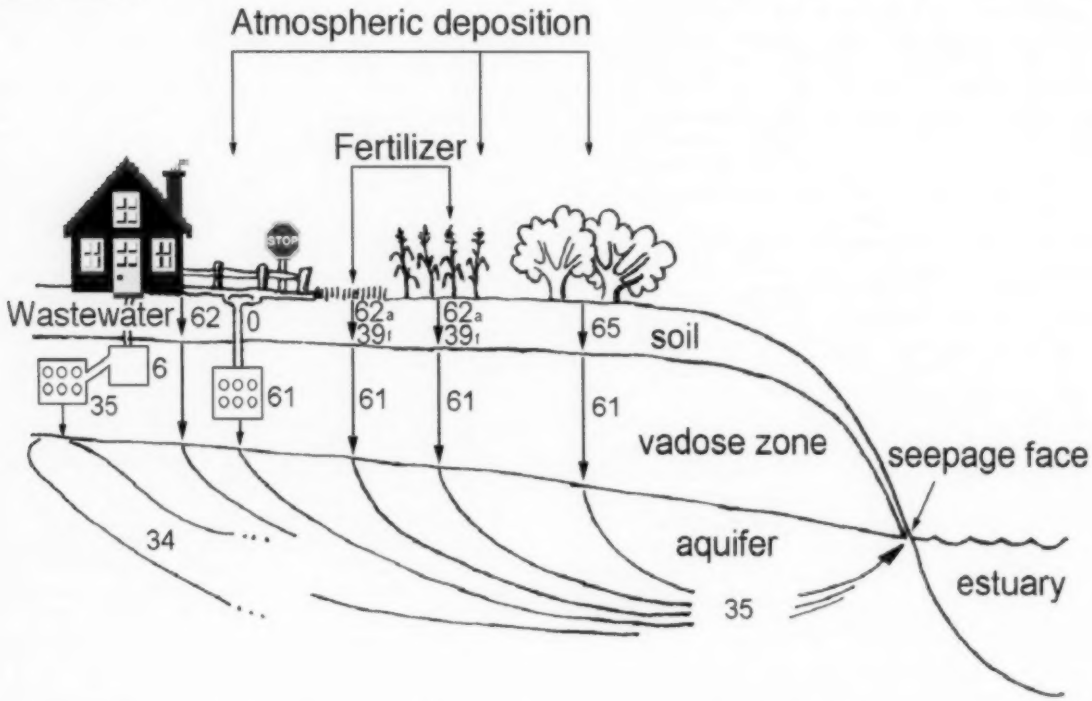
Fig. 2. Schematic diagram of the sources, land covers, and components of the watershed ecosystem that are included in the Waquoit Bay nitrogen-loading model (NLM). The numbers show losses of total nitrogen incurred as the nitrogen travels through the various components; *a* denotes the percentage of atmospheric nitrogen and *f* the percentage of fertilizer nitrogen lost as it passes through agriculture land covers. All numbers indicate percent loss of nitrogen entering each component (soil, vadose zone, aquifer, septic tank, leaching system, or storm drain). (From Valiela et al. 2000*a*, reproduced with permission of Biogeochemistry, Vol. © 2000 Kluwer Academic Publishers.)



deposition of organic nitrogen. Once we had established the reconstructed rate of nitrogen deposition, we applied it to the land-use mosaics of the Waquoit Bay watershed and used NLM to track the losses that occurred as the nitrogen traversed each land-use type.

Fertilizer use

Two pieces of information were required to estimate the nitrogen contribution from fertilizers. We needed to know the amount of fertilizer being applied to a given crop and the area of that crop within the watershed being modeled. Ideally, there would be historical records of fertilizer-application rates on all of the individual parcels within the watershed that was being modeled. However, that information is lacking, so as a reasonable alternative we estimated the fertilizer-application rate by using regional trends (USDA 1993, 1999) and applied that rate to the known land uses specific to our watershed.

We first obtained a regional estimate of historical changes in fertilizer-application rates using data for the northeastern U.S.A. (USDA 1993, 1999). We obtained estimates of total fertilizer consumption in New England and New York from 1900 to 1990, and of the total land area dedicated to major fertilized field crops (hay, corn, wheat, oats, and barley; USDA 1999). We then divided the total amount of fertilizer applied by the area under cultivation to roughly estimate fertilizer-application rates ($kg \cdot ha^{-1}$) for these major field crops.

We applied the application rates developed for major crops to locally appropriate modern rates. On Cape Cod, fertilizers are more frequently used on smaller scale horticultural crops, lawns, golf courses, and cranberry bogs, but historical data comparable to those concerning fertilization of field crops were not readily available. In the absence of detailed data, we estimated the time course of fertilizer use for these other crops by using the historical trend line calculated for major field crops to backcast across the decades, starting from modern application rates. Cranberries are much less intensively fertilized than many other agricultural crops, so we used agricultural reports and bulletins produced throughout the century by the Massachusetts Cranberry Experiment Station to generate an independent time course for the use of fertilizers on cranberry bogs (Demoranville 1996).

Wastewater disposal

In some environments the distinction between wastewater nitrogen inputs and fertilizer nitrogen inputs is unclear. If a large portion of fertilized crops grown in a watershed is consumed in that watershed, then including both fertilizer and wastewater terms could overestimate the amount of nitrogen entering the system because the wastewater nitrogen would not be a new source of nitrogen but would be nitrogen transformed from the fertilizer inputs. In the Waquoit Bay watershed, as with many suburban landscapes, the vast majority of the foods that are consumed are imported from elsewhere. Thus, we feel justified in regarding wastewater nitrogen as a separate source of new nitrogen.

We assessed changes in wastewater-derived nitrogen according to the number of houses in the watershed, which was determined from aerial photographs taken in each of the years to be studied. Wastewater in the Waquoit Bay watershed is disposed of via on-site septic systems. We assumed a mean annual occupancy rate of 1.79 people per house (Valiela et al. 1997*a*). This occupancy rate

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reflects the seasonal nature of Cape Cod, where many residences are occupied only on weekends or in the summer (Valiela et al. 1997*a*). A compilation of literature values indicated that individuals release a mean of 4.8 kg N·year^{-1} (Valiela et al. 1997*a*). From the occupancy rate, number of houses, and amount of nitrogen produced per person each year, we calculated the total amount of wastewater-derived nitrogen released within the Waquoit Bay watershed.

Effect of historical changes in loads on eutrophication within the estuaries

To understand how changes in land use affect the ecology of coastal embayments, we used the time courses for each major source of nitrogen described above and entered the data into NLM to develop a historical trend in nitrogen loading into Waquoit Bay. To examine the ecological impact of the change in nitrogen loads we first used a space-for-time substitution to depict the changes that have occurred in the biomass of the three dominant primary producers, phytoplankton, macroalgae, and eelgrass (*Zostera marina*), in different estuaries of the Waquoit Bay estuarine complex that are currently exposed to different nitrogen loads. We used previous studies on phytoplankton and macroalgal biomass in the different sub-estuaries of Waquoit Bay for the space-for-time substitution (Valiela et al. 2000*b*). We then used our historical reconstruction of loads from the Waquoit Bay watershed, plus aerial photographic evidence (Costa 1988) and visual surveys (Short and Burdick 1996) of seagrass cover, to assess how urbanization may have affected the ecology of the Waquoit Bay estuarine system. Finally, we traced the changes that have occurred in the estuary to the level of animals by looking at historical changes in the scallop harvest as a proxy for changes in the food webs of receiving estuaries.

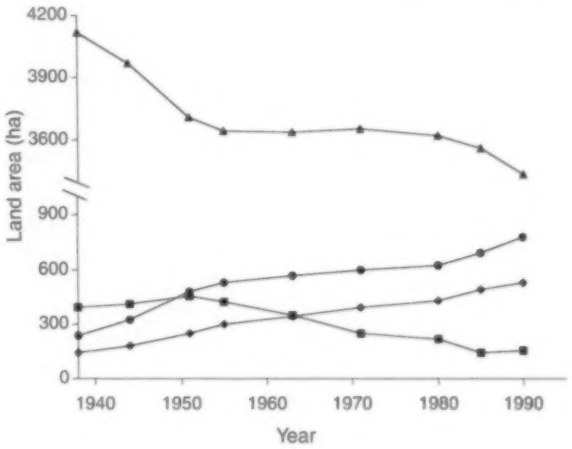
Results and discussion

Substantial changes have occurred in the Waquoit Bay watershed during the last several decades as the watershed became more urbanized. Below we examine the changes in the land-use mosaic, as well as how the sources of nitrogen have changed, how that is reflected in the nitrogen load entering Waquoit Bay, and how the ecology of the Bay has changed as a result of the alteration of land use in its watershed during the last 60 years.

Changes in the land-use mosaic

Land use in the Waquoit Bay watershed changed substantially between 1938 and 1990 (Fig. 3). The areas of fertilized turf (golf courses, lawns, and other turf areas) and impervious surfaces (roads, roofs, driveways, and parking lots) within the watershed have all increased since 1938. These increases are largely associated with urbanization. Lawns accounted for 33% of the increase in turf area between 1938 and 1990. An additional 58% of the increase in turf area is classified as "other," but this is predominantly associated with an increase in turf area surrounding the Massachusetts Military Reservation at the northern extreme of the watershed. The golf courses in the Waquoit Bay watershed account for only 6% of the total turf area and less than 1% of the total land area. Roads, roofs, and driveways account for 44% of the increase in area of impervious surfaces. The remaining increases in impervious-land area result mostly from increases in the number of parking lots associated with commercial developments within the watershed, as well as commercial areas and runways in the Massachusetts Military Reservation.

Fig. 3. Changes in land use within the Waquoit Bay watershed from 1938 to 1990. Turf area (●) includes lawns, golf courses, and parks. Impervious surfaces (◆) include roads, roofs, driveways, and parking lots. Agricultural land (■) includes horticultural areas and cranberry bogs. Natural vegetation (▲) is calculated as the total land area minus all non-natural land covers.



Pressure for residential use of land parcels has caused losses of naturally vegetated areas, cranberry bogs, and other agricultural areas since the 1930s (Fig. 3). Naturally vegetated lands decreased from 84% of the total land area in the Waquoit Bay watershed in 1938 to only 68% in 1990. Agricultural areas and cranberry bogs also decreased from a peak of 553 ha in 1955 to only 225 ha in 1990.

Changes in nitrogen sources

Atmospheric deposition

Wet deposition of ammonium decreased significantly (F = 34.6, $P < 0.01$; Bowen and Valiela 2001) through the century, while wet deposition of nitrate increased significantly (F = 53.9, $P < 0.01$; Bowen and Valiela 2001; Fig. 4*a*). The shift in dominance between ammonium and nitrate wet deposition may be another consequence of increased urbanization in the northeastern U.S.A., since anthropogenic ammonium deposition is largely due to emissions from livestock waste and fertilized soils (Dentener and Crutzen 1994), both of which have decreased regionally over the last half of the 20th century. The largest anthropogenic source of NO_x emissions is the combustion of fossil fuels during industrial and commercial processes and in gasoline engines. Nitrogen from all of these sources has increased as a result of increased urbanization on Cape Cod (Bowen and Valiela 2001), and the increased industrialization of the Midwest, whose NO_x emissions contribute substantially to atmospheric deposition in the northeastern U.S.A. (Dennis 1995).

Total nitrogen deposition to the Massachusetts area increased significantly ($y = 0.026x - 39.4$, $F = 41.2$, $P < 0.01$) during the 20th century, by a rate of around 0.26 kg N·ha^{-1} per decade (Fig. 4*a*), and is presently approximately 12 kg N·ha^{-1}· year^{-1}. The vertical lines in Fig. 4*a* show the stan-

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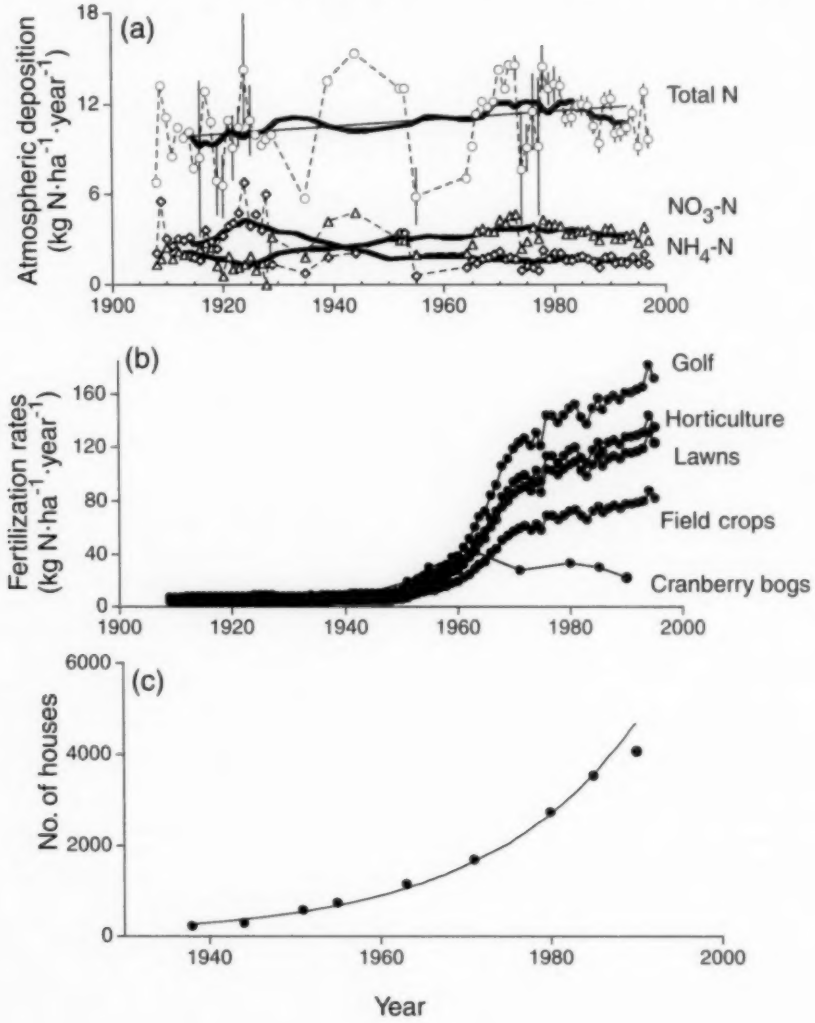
Fig 4. (*a*) Ammonium (NH_4-N), nitrate (NO_3-N), and total nitrogen deposition onto the Cape Cod area from 1910 to 1995. Data for ammonium (◇) and nitrate (△) represent wet deposition only; total nitrogen (○) includes estimates of dry deposition and deposition of organic nitrogen. The symbols represent the year-to-year data and the thick line is the 10-year moving average of the data. Error bars are included for total nitrogen when data are from more than one study (data from Bowen and Valiela 2001). (*b*) Reconstructed trends in fertilizer-application rates on golf courses, horticultural crops, lawns, field crops, and cranberry bogs in the northeastern U.S.A. between 1910 and 1995. (*c*) Numbers of houses in the Waquoit Bay watershed between 1938 and 1990 ($Y = 0.0 \times 10^{0.02x}$, $R^2 = 0.99$).



dard deviation of the means for total nitrogen in years for which more than one value was reported in the literature. The mean standard deviation for any one point estimate of total deposition is 3.24 kg $N \cdot ha^{-1} \cdot year^{-1}$. Our interest was to define a long-term trend; we can assess the uncertainty in the slope of the regression fitted to the entire data set by the ratio of the standard error of the slope, 0.009, relative to the slope of the regression, 0.026. This coefficient of variation was 34% of the slope. This represents considerable uncertainty, but does not prevent the regression from being significant.

There is some ambiguity in interpreting these loads because there is a question about the lability of the organic component of atmospheric nitrogen. The conventional wisdom has always been that organic nitrogen is largely refractory and so its role in ecological processes must be modest. Seitzinger and Sanders (1999) suggest that 45–75% of atmospheric organic nitrogen could be labile. In Waquoit Bay we find that forested watersheds contribute groundwater that is high in organic nitrogen (Valiela et al. 2000*b*), but the receiving estuaries are not eutrophic. This suggests that atmospherically derived organic nitrogen might be less biologically available than organic nitrogen from urbanized watersheds. The lability of atmospheric DON thus still needs study.

The magnitude of the nitrogen load from the atmosphere is of some significance, because at certain rates of deposition

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the ability of the forest to intercept atmospheric nitrogen declines, a phenomenon described as nitrogen saturation (Aber et al. 1989; Nadelhoffer et al. 1995). Evidence of nitrogen saturation was visible in some Welsh forests when total nitrogen inputs exceeded 10 kg·ha^{-1}·year^{-1} (Emmett et al. 1993). When total nitrogen deposition exceeded 25 kg·ha^{-1}·year^{-1} all sites studied displayed nitrogen leaching (Dise and Wright 1995). Our reconstructed record of nitrogen deposition indicates that Cape Cod forests are receiving inputs of atmospheric nitrogen that are high enough to induce nitrogen saturation. If there are additional increases in the deposition of total atmospheric nitrogen, this will inevitably result in further leaching of nitrogen to coastal waters.

Fertilizer use

From 1913, when the first commercial ammonium factory opened, until the 1940s, less than 4.5 t of fertilizers were synthesized (Smil 1997). Today roughly 80 million t are being produced globally (Smil 1999). The use of nitrogen fertilizers in the northeastern U.S.A. increased markedly during the same time period. The mean dosage of fertilizer applied to field crops in the northeastern U.S.A. was relatively constant between 1910 and 1940, but has since risen sharply, increasing from less than 10 kg N·ha^{-1}·year^{-1} in 1950 to 80 kg N·ha^{-1}·year^{-1} in recent years (Fig. 4*b*). The rate of increase in fertilizer production appears to be slowing, both in New England (Fig. 4*b*) and globally (Frink et al. 1999).

Fertilizer-application rates to non-agricultural lands can be even higher than application rates to some crops. We estimated secular trends in fertilizer-application rates for most of the dominant uses of fertilizer on Cape Cod. Fertilizer application to turf, particularly golf courses, involves the largest dosages of nitrogen (161 kg·ha^{-1}·year^{-1}; Correll et al. 1992), followed by applications of nitrogen to horticultural crops (136 kg·ha^{-1}·year^{-1}; Petrovic 1990) and lawns (122 kg·ha^{-1}·year^{-1}; Valiela et al. 1997*a*). Today only 20–25 kg N·ha^{-1}·year^{-1} is applied to cranberry bogs, a decrease from a peak of about 45 kg N·ha^{-1}·year^{-1} in the 1960s (Demoranville 1996).

Wastewater disposal

Pressure for residential use of land can be seen in the rise in the number of houses in the Waquoit Bay watershed during the last 60 years (Fig. 4*c*), from fewer than 250 to more than 4000. The total amount of wastewater generated within the Waquoit Bay watershed increased from just over 2000 kg N·year^{-1} in 1938 to almost 30 000 kg N·year^{-1} in 1990, a factor of almost 17. This sharp increase demonstrates the impact of urban sprawl on these coastal watersheds.

Nitrogen loading into Waquoit Bay

Total nitrogen inputs into the Waquoit Bay watershed increased almost twofold between 1938 and 1990 (Fig. 5*a*). Atmospheric deposition has been the predominant contributor of nitrogen to the watershed during the last 60 years, but the magnitude of this deposition onto the Waquoit Bay landscape has remained surprisingly uniform throughout the century. The relative importance of atmospheric deposition has decreased: in 1938 atmospheric deposition onto the watershed accounted for 95% of the nitrogen input, but in 1990 it accounted for only 59% of total nitrogen delivery. Wastewater and fertilizer were minor sources of nitrogen in midcentury, but increased to 22 and 19% of the total contribution, respectively (Fig. 5*a*, Table 1). It was clearly the increase in wastewater and fertilizer nitrogen that was responsible for the increase in nitrogen load between 1938 and 1990.

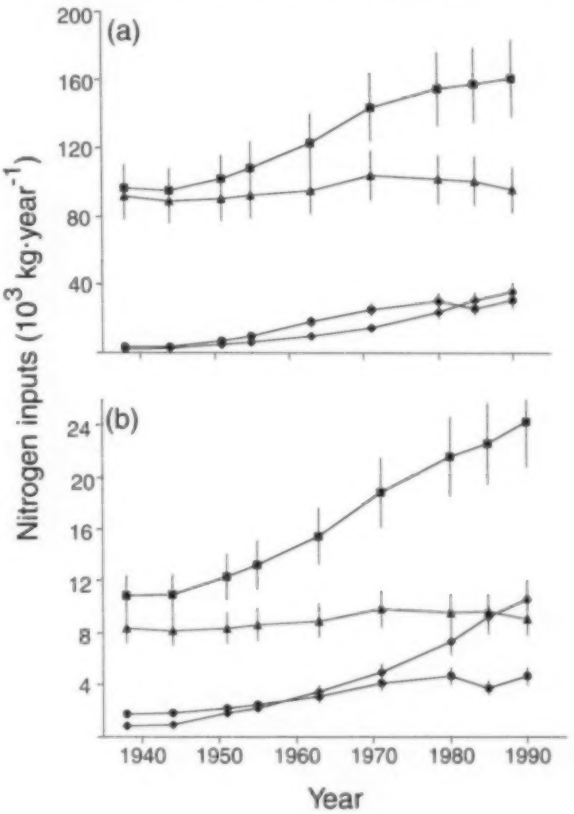

Fig. 5. Modeled historical nitrogen loads into the watershed (*a*) and estuary (*b*) of Waquoit Bay. The total nitrogen loads (■) are broken down according to the three major sources of nitrogen: atmospheric deposition (▲), wastewater disposal (◆), and fertilizer application (●). Data are plotted with the 14% standard error that is associated with the Waquoit Bay NLM (Valiela et al. 1997*a*).

After losses and transformations that occur during transport through the landscape and aquifer are accounted for, NLM calculations showed that delivery of nitrogen to the estuary more than doubled from 1938 to 1990 (Fig. 5*b*, Table 1). Atmospheric deposition accounted for 77% of the total nitrogen delivered to Waquoit Bay in 1938 and only 37% of the load in 1990. Wastewater derived from on-site septic systems increased by a factor of more than 12, and in 1990 accounted for 43% of all of the nitrogen entering Waquoit Bay (Table 1). Wastewater, because it is subject to lower losses within the watershed, became the most important source of nitrogen entering the estuary during the 1980s, despite the fact that atmospheric nitrogen was the largest source of nitrogen entering the watershed.

The relative contributions by wastewater disposal, fertilizer use, and atmospheric deposition to nitrogen loading into

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Table 1. Relative contributions of the major sources of nitrogen entering the Waquoit Bay estuary in 1938 and 1990.

Source of nitrogen	1938 nitrogen load		1990 nitrogen load	
	$\times 10^3$ kg·year^{-1}	%	$\times 10^3$ kg·year^{-1}	%
Entering the watershed				
Atmospheric deposition	91.3	95	95.5	59
Wastewater disposal	2.1	2	35.7	22
Fertilizer use	3.2	3	30.5	19
Total	96.6	100	161.7	100
Entering the estuary				
Atmospheric deposition	8.4	77	9.1	38
Wastewater disposal	0.7	7	10.5	43
Fertilizer use	1.7	16	4.7	19
Total	10.9	100	24.3	100

Note: The propagated standard error of the modeled nitrogen load is 14% (Valiela et al. 1997*a*). The percent contribution from each nitrogen source is slightly different from values published in Valiela et al. (1997*a*). The differences result from the need to use regional trends in order to incorporate historical changes. In some instances these regional trends were slightly different from the specific information on Waquoit Bay used in the original publication. The difference between the regional approach and Valiela et al.'s (1997*a*) results fall within the standard error of the model.

Table 2. Percent contributions of the major sources of nitrogen to various Massachusetts and Rhode Island coastal ponds.

Estuary	Source of nitrogen (%)		Population density (no. of people·ha^{-1})	
	Wastewater	Fertilizer	Atmosphere	
Sage Lot Pond, Mass.	5	46	49	0.21
Trustom Pond, R.I.	17	70	13	0.75
Cards Pond, R.I.	21	68	11	0.96
Waquoit Bay, Mass.	43	20	37	1.45
Mashpee River, Mass.	49	15	36	1.81
Green Pond, Mass.	54	25	21	1.81
Pt. Judith Pond, R.I.	55	36	9	2.14
West Falmouth Harbor, Mass.	64	6	30	2.47
Childs River, Mass.	60	12	28	2.54
Green Pond, R.I.	47	43	10	3.65
Potter's Pond, R.I.	50	39	11	4.62
Coastal ponds (mean ± SD)	42 ± 19	35 ± 21	23 ± 13	2.03 ± 1.3
Contribution from northeastern U.S.A. to North Atlantic Ocean[a]	33 (26)	22 (17)	44 (34)	0.87

Note: Data for Rhode Island Pond are from Lee and Olsen (1985) and Nixon et al. (1982) and are based on 1981 land use. Data for Massachusetts are modeled using the Waquoit Bay nitrogen-loading model (NLM) and are based on 1990 land use. Data for Green Pond are from Kroeger et al. (1999). Data for the northeastern U.S.A. are from Howarth et al. (1996).

[a]Howarth et al. (1996) include biological nitrogen fixation as a source that contributes 23% of the nitrogen to the North Atlantic Ocean. Numbers in parentheses show the percent contribution from biological nitrogen fixation; non-parenthetical numbers do not include biological fixation.

estuaries throughout the northeastern U.S.A. vary (Table 2). Nitrogen contributions from wastewater range from 5 to 64% of the total nitrogen load, those from fertilizer range from 6 to 70%, and those from atmospheric deposition range from 9 to 49%. There is variation from one estuary to another, but the specific value depends on the size of and relative land uses in the watershed. In some cases, inputs of agricultural fertilizers are dominant. Chesapeake Bay, for example, receives 36% of its nitrogen from fertilizers (Hinga et al. 1991), and large portions of the Chesapeake Bay watershed are under agricultural land use. Elsewhere, urban sprawl drives the increased nitrogen inputs. In Massachusetts and Rhode Island estuaries the percent contributions of wastewater disposal and population density (Table 2) generally increased together. In general, although there is some variation from one watershed to another, the mean contribution of nitrogen from wastewater disposal, atmospheric deposition, and fertilizer use to these estuaries is statistically similar to the calculated loads from the entire northeastern U.S.A. (Howarth et al. 1996).

Impact on producer communities and estuarine food webs

The link between land uses, nitrogen loads, and estuarine

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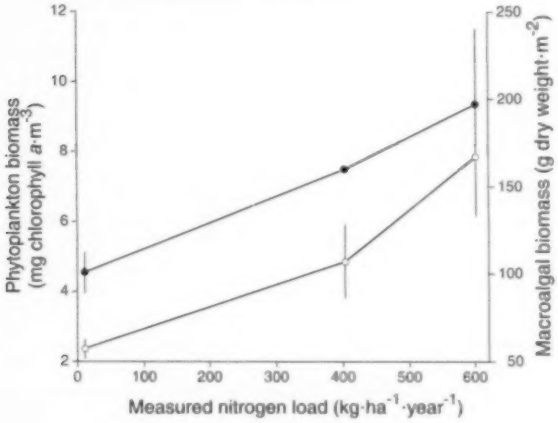
Fig. 6. Biomass of phytoplankton (●) and macroalgae (○) in estuaries with increasing nitrogen loads. From left to right the estuaries are Sage Lot Pond, Quashnet River, and Childs River. Data are taken from Valiela et al. (2000*b*).



food webs has been established using stable-isotopic evidence in estuaries receiving different nitrogen loads. This linkage occurs because wastewater-derived nitrogen has a higher ^{15}N isotopic signature than nitrogen derived from either atmospheric or fertilizer sources (Gormly and Spaulding 1979; Kreitler 1979). As the proportion of the watershed that is urbanized increases, so does the isotopic signal in the groundwater and in the water column (McClelland and Valiela 1998). When that nitrogen is incorporated by estuarine producers, the heavy ^{15}N signal is incorporated as well, so producers in estuaries receiving a greater proportion of wastewater-derived nitrogen have heavier isotopic signals than producers in pristine estuaries (McClelland and Valiela 1998). The ^{15}N signal can even be traced through both primary and secondary consumers (McClelland and Valiela 1998). Thus, it is possible to directly follow the nitrogen derived from wastewater through the entire food web in estuaries. The incorporation of wastewater-derived nitrogen into the producer and consumer populations, however, does not necessarily indicate that there have been alterations in the structure of estuarine food webs. Were the changes in land use sufficient to alter the ecology of the receiving estuaries?

The biomass of phytoplankton and benthic macroalgae in Waquoit Bay increased across a range of estuaries receiving increasingly higher nitrogen loads (Fig. 6). These direct responses to nitrogen enrichment (Valiela et al. 1997*b*) have several indirect repercussions for the rest of the ecosystem. Phytoplankton and macroalgal mats derive their nutrients largely from the water column. Seagrasses, however, tend to be light, rather than nutrient, limited (Duarte 1995). When nitrogen is added to estuaries, because of their increased growth, phytoplankton and macroalgae intercept increasing portions of light, thereby limiting light availability for seagrasses (Hauxwell et al. 2001).

Growth, areal cover, and biomass of eelgrass diminished in response to increases in phytoplankton and macroalgal biomass (Hauxwell et al. 2001). Areal cover of eelgrass, when viewed across a range of northeastern U.S. estuaries, was sharply reduced at nitrogen loads greater than 20 kg·ha^{-1}·year^{-1}; the meadows disappeared by the time nitrogen loads exceeded 100 kg·ha^{-1}·year^{-1} (Fig. 7*a*). Temporal changes that have occurred during the last 60 years in Waquoit Bay also demonstrate a sharp decline in eelgrass area (Fig. 7*b*). Before the 1950s, eelgrass was still recovering from the near-complete loss caused by the wasting disease of the early 1930s (Renn 1935). Note also that during the 1930–1950 period, nitrogen loads were lower than the 20 kg·ha^{-1}·year^{-1} that we posit as a threshold for the survival of eelgrass meadows. The building boom on Cape Cod during the 1960s resulted in an increase in nitrogen loads, so that by the early 1970s, the nitrogen load exceeded 20 kg·ha^{-1}·year^{-1}, eelgrass meadows were notably smaller in area, and the loss of eelgrass habitat continued through 1990. The historical reconstruction indicates that the nitrogen loads corresponding to near complete destruction of eelgrass meadows ranged only between 15 kg and 30 kg·ha^{-1}·year^{-1} (Fig. 7*b*).

Since the presence of seagrass is required for the maintenance of many taxa, including commercially important shell- and fin-fish species, changes in eelgrass cover imply drastic changes in the rest of the food webs in affected estuaries. For example, the bay scallop (*Argopecten irradians*), a commercially important shellfish species, is closely dependent on eelgrass habitat. During the time-span when the eelgrass meadow area decreased (Fig. 7*b*), the annual harvest of bay scallops in Waquoit Bay decreased by three orders of magnitude, from over 100 000 L·year^{-1} in the early 1960s to under 100 L·year^{-1} in recent years (Fig. 8*a*). The decline in the annual scallop harvest correlated with an increase in nitrogen loads (Fig. 8*b*). Ryther and Dunstan (1971) reported a similar loss of oysters and hard clams as a result of nutrient enrichment from the Long Island duckling industry in Moriches Bay, N.Y. We can therefore claim that changes in land use in watersheds, to urban sprawl in particular, can be demonstrably linked to a drastic restructuring of estuarine ecosystems.

Implications for the management of coastal watersheds

The historical reconstruction of land-derived nitrogen loads, plus the linking of these loads to sensitive indicators such as eelgrass meadows and bay scallops, provides some means to identify management priorities as well as define management end-points. If management goals include a reduction of nitrogen loads, the results of this work suggest some general approaches which could be used to remediate the increased nitrogen loads that are the result of urban sprawl in coastal watersheds.

Preservation of green open space on land can make a contribution to the management of nitrogen loads. Atmospheric-nitrogen deposition is still the largest nitrogen source in the watershed of Waquoit Bay. Interception of atmospheric nitrogen is highest where natural vegetation covers land parcels, and this feature needs to be a part of the tool kit of a manager thinking about the coastal zone. Preservation of green space may slow the increase in nutrient enrichment to receiving waters by intercepting atmospheric deposition, and also by limiting the supply of nitrogen that would result from conversion to other land uses like agriculture or residential building.

Management of wastewater and restriction of the use of fertilizers are the most practical measures available locally to lower nutrient enrichment. Zoning restrictions, improve-

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Fig. 7. (*a*) Percentage of eelgrass area lost as a function of nitrogen load. The data, for various Massachusetts estuaries, are taken from Valiela et al. (2001). (*b*) Percentage of area covered with eelgrass in Waquoit Bay estimated from aerial photographs taken between 1940 and 1989 (Costa 1988; Short and Burdick 1996) plotted against modeled historical nitrogen loads.

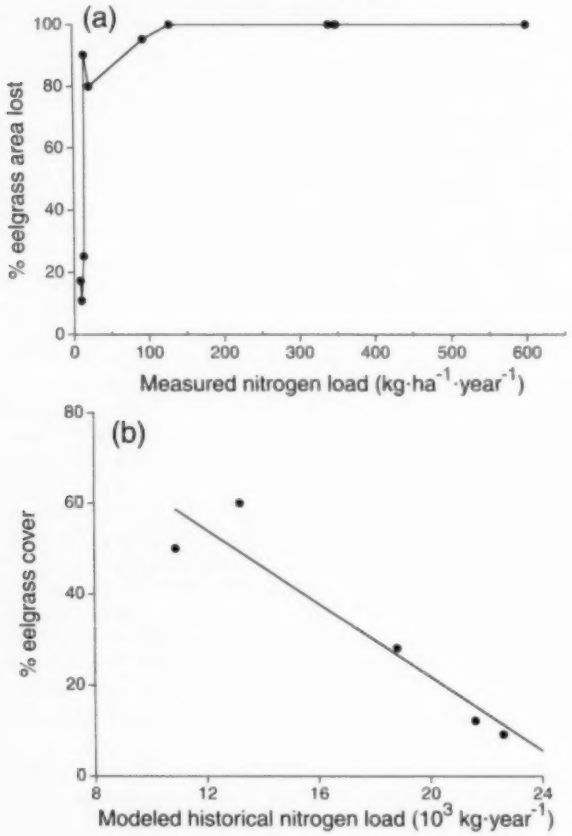
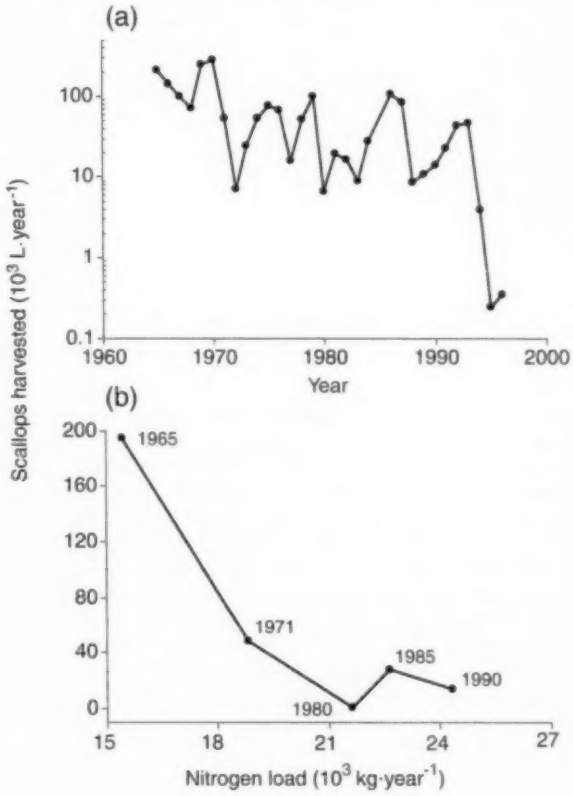


Fig. 8. (*a*) Amounts of scallops reported to have been harvested in Waquoit Bay from 1960 to 1997. (*b*) Volumes of scallops reported to have been harvested in Waquoit Bay as a function of the modeled historical nitrogen loads from this reconstruction. Data are from the Shellfish Warden's annual report included in the Town of Falmouth Annual Reports.



ment of in situ septic systems, or installation of small sewage-treatment plants could all lower the inputs of wastewater nitrogen. Restricting the use of fertilizers and area of turf will also, to a small degree, lower nitrogen inputs, but could be especially effective in areas with more intensive agriculture. Choice of the appropriate management option depends on the target a community wants to achieve. Stakeholders might decide, for example, that they would like to restore eelgrass to 50% of their estuary. Then, modeling such as we have done in this paper could identify the nitrogen load that was present at the time when such eelgrass cover existed, and indicate the pathways that would possibly reduce nitrogen loads.

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Spatial covariation in survival rates of Northeast Pacific pink salmon (*Oncorhynchus gorbuscha*)

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Abstract: We examined spatial patterns of covariation in indices of survival rate (residuals from the best-fit stock–recruitment curve) across four decades among 43 wild pink salmon (*Oncorhynchus gorbuscha*) stocks from 14 geographical regions in Washington, British Columbia, and Alaska. We found strong evidence of positive covariation among stocks within each region and between certain adjacent regions (e.g., correlations from 0.3 to 0.7) but no evidence of covariation between stocks of distant regions (e.g., separated by 1000 km or more). This suggests that important environmental processes affecting temporal variation in survival rates of pink salmon from spawners to recruits operate at regional spatial scales rather than at the larger ocean basin scale. Based on limited fry abundance data, we found that this covariation in spawner-to-recruit survival rates may be strongly influenced by marine processes.

Résumé : Nous avons examiné la structure spatiale de la covariation des indices des taux de survie (résidus de la courbe stock–recrutement la mieux ajustée) sur une période de 40 ans chez 43 stocks sauvages de Saumons roses (*Oncorhynchus gorbuscha*) de 14 régions géographiques du Washington, de la Colombie-Britannique et de l'Alaska. Il existe de fortes indications de l'existence d'une covariation positive entre les stocks dans chacune des régions et entre certaines régions adjacentes (e.g., des corrélations de 0,3 à 0,7), mais aucune évidence de covariation entre les stocks de régions éloignées (e.g., séparées par 1000 km ou plus). Cela laisse croire que d'importants mécanismes environnementaux, qui affectent la variation temporelle des taux de survie des géniteurs aux recrues chez le Saumon rose, agissent à des échelles spatiales régionales plutôt qu'à l'échelle plus large du bassin océanique. Des données restreintes sur l'abondance des alevins nous amènent à conclure que cette covariation dans la survie des géniteurs aux recrues est peut-être fortement influencée par les processus marins.

[Traduit par la Rédaction]

Introduction

Pacific salmon (*Oncorhynchus* spp.) exhibit large interannual variation in survival rates from eggs to adults. Stock–recruitment relationships (i.e., density-dependent effects) usually explain little of this variation, suggesting that environmental influences are important (Peterman 1987). Although numerous studies have identified relationships between physical and biological variables and survival rates of salmon during freshwater, estuarine, or marine life stages, these studies have typically been based on data for single stocks and limited years (for reviews, see Groot and Margolis 1991; Pearcy 1992). Such relationships tend to break down as new data are gathered or other stocks are examined (Myers 1998).

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Recently, researchers have explored patterns of covariation in survival rates among groups of fish stocks as a powerful method for generating hypotheses about the spatial characteristics of environmental processes that affect survival rates of fish (e.g., Myers et al. 1997; Peterman et al. 1998; Botsford and Paulsen 2000). For example, Peterman et al. (1998) examined covariation in spawner-to-recruit (SR) survival rates of 29 sockeye salmon (*O. nerka*) stocks from British Columbia (B.C.) and Alaska. They found positive covariation among Fraser River (B.C.) stocks and, to a greater extent, among Bristol Bay (Alaska) stocks but no evidence of covariation between these two regions or with stocks of other regions in B.C. and Alaska. Their results suggest that some important environmental processes affecting survival rates of sockeye salmon are confined to regional spatial scales and that the shared influence of these processes appears to act primarily during the marine life stage (Peterman et al. 1998).

In this paper, we use a similar approach to that of Peterman et al. (1998) to examine spatial patterns of covariation in survival rates of pink salmon (*O. gorbuscha*) stocks in the Northeast Pacific. Two recent papers have explored aspects of this topic (Myers et al. 1997; Blackbourn 1998). In their analysis of numerous fish species, Myers et al. (1997) provided single statistics to characterize the spatial scale of covariation among 32 time series of SR survival rates of pink salmon and among 10 time series of freshwater (spawner-to-fry) survival rates. In contrast, Blackbourn

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(1998) examined correlations among 15 time series of marine (fry-to-recruit) survival rates for pink salmon. We extended these analyses by much more comprehensively investigating spatial patterns of covariation among pink salmon. First, we used a unique data set in terms of number of stocks, duration of time series, and extent of geographical coverage to rigorously define the magnitude and spatial extent of covariation in SR survival rates. Second, we used powerful randomization tests to assess the statistical significance of covariation among replicate stocks within and between designated regions. Third, we examined covariation in freshwater survival rates among nine wild stocks and in marine survival rates among 20 wild and hatchery stocks. Last, we explored the relative contribution of freshwater and marine processes in driving covariation among SR survival rates.

These analyses will help guide future research on examining relationships between survival rates of pink salmon and environmental variables. In particular, our tests of various hypotheses about spatial patterns of covariation in survival rates will assist in identifying appropriate spatial characteristics of candidate environmental variables that might affect those survival rates. Such inferences will also identify appropriate groups of stocks that can be used in multistock analyses to increase statistical power and reliability of estimated effects. Such relationships should help researchers develop better models for evaluating alternative management policies (e.g., escapement goals or conservation measures) and forecasting abundance of pink salmon or effects of future climate change.

Methods

Data

To estimate annual survival rates, we used abundance data for spawners and recruits (catch plus escapement) for 43 wild pink salmon stocks or stock groups (Table 1). To facilitate analyses, these 43 stocks were grouped into 14 management areas or geographical "regions" (Fig. 1; Table 1). Note that only one data set was available for each of the Fraser River, Mainland B.C., and Bristol Bay regions. In most cases, data sets represent annual escapement and catch summed across groups of adjacent populations because catch cannot be accurately allocated to more discrete spawning populations. As a result, there is a wide range in average recruitment among data sets, from a low of 38 000 for pink salmon populations in Statistical Area 10 of the Central B.C. region to a high of nearly 31 million for the southern districts of Southeast Alaska (Table 1). Methods for estimating spawner abundance varied across data sets: a mix of foot and float surveys for Washington stocks, mark–recapture studies and foot surveys for the Fraser River stock, mostly foot surveys for the remaining B.C. stocks, and mostly aerial surveys for Alaska stocks. Although we originally obtained more than 43 spawner–recruit data sets, we combined some data sets and excluded others to minimize potential errors in allocation of catch. In particular, only those data sets with 15 or more brood years were included to ensure a reasonable sample size when computing correlations.

For the Kodiak Island region, we obtained data sets for five districts over brood years 1980–1996 (Table 1). These were used in the "stock-specific" correlation analyses described below to provide replication for this region. However, an additional and much longer data set (brood years 1962–1996) was obtained for total escapement and catch across districts in the Kodiak region (denoted "Across Districts" in Table 1). We used this data set in analyses of "region-specific" indices (described below) to provide 18 additional years of data.

Measures of fry abundance were obtained for nine wild and 13 hatchery stocks in B.C. and Alaska, which represent seven of the 14 regions defined for stock–recruit data (Table 2). In general, hatchery data sets were considerably shorter than stock–recruit data sets. We were therefore less restrictive and used hatchery data sets with 10 or more years of data (rather than 15 years) to provide additional replication.

Statistical analyses

Indices of survival rate

For each stock–recruit data set (Table 1), we calculated a normalized index of spawner-to-recruit survival rate (SR index) that removed possible within-stock density-dependent effects. This index was the time series of brood year residuals (i.e., deviations) from the fit of a stock–recruitment model. For each data set, we fit both the Beverton–Holt and the Ricker stock–recruitment models to $\log_e$(recruits per spawner) as a function of spawner abundance. Although the Ricker model is traditionally used for Pacific salmon data, the Beverton–Holt model performed best across data sets based on the AIC_c model-selection criterion (Akaike information criterion corrected for small sample sizes; Hurvich and Tsai 1989). Thus, most results are reported for SR indices (residuals) from Beverton–Holt fits; however, as discussed below, very similar results were obtained for SR indices derived from the Ricker model.

Similarly, for each of the nine wild stocks with fry abundance data (Table 2), we calculated a freshwater survival rate index (time series of residuals) from fits of stock–recruitment models to $\log_e$(fry per spawner) as a function of spawner abundance. Again, we examined both the Beverton–Holt and the Ricker models, and the Ricker model was clearly the best model across data sets based on AIC_c.

Last, we computed indices of marine survival rate for 20 wild and hatchery stocks with fry data by fitting stock–recruitment models to $\log_e$(recruits per fry) as a function of fry abundance. The Sashin Creek and Auke Creek wild data sets were omitted due to the lack of catch data. For the marine survival rate index, we used residuals from fits of the Beverton–Holt model, which performed best across stocks based on AIC_c. Note that for wild stocks with preemergent fry data (all stocks except Fraser River) (Table 2), this "marine" survival rate index also contains a component of late freshwater survival (i.e., from the time at which preemergent fry densities are measured to the point of ocean entry).

Patterns of covariation

To examine spatial patterns of covariation in SR indices, we calculated Pearson product-moment correlation coefficients for all pairwise comparisons among the 43 SR indices of the 14 regions. Correlations were only computed between data series with 15 or more years in common. Because there was little evidence of widespread autocorrelation in the 43 SR indices (Table 1), we tested pairwise correlations using a standard significance test rather than adjusting test statistics to account for autocorrelation (Pyper and Peterman 1998). Unless reported otherwise, all tests of statistical significance, including the randomization tests discussed below, were conducted for two-tailed tests with $\alpha = 0.05$.

To facilitate presentation of results, correlations among SR indices were summarized by region. Specifically, average correlations are reported for comparisons either within or between regions when there was more than one pairwise correlation. As described below, randomization tests were used to test the statistical significance of these average correlations.

Next, because we found strong evidence of positive covariation within each of the 11 regions with replicate SR indices, we combined the SR indices of each region into a single "aggregated" in-

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Table 1. Summary of data sets for 43 wild pink salmon stocks used to compute SR survival rate indices.

Region	Stock or district (D)	Brood years	*N*	*R*	*H*	Lag1	Source[a]
Washington (WA)	Nooksack[b]	1959–1995	19	154	0.60	–0.17	1
	Skagit[b]	1959–1995	19	889	0.48	–0.16	1
	Stillaguamish[b]	1959–1995	19	293	0.42	–0.01	1
	Snohomish[b]	1959–1995	19	258	0.41	0.06	1
	Puyallup River[b]	1959–1995	19	46	0.49	0.17	1
	Hood Canal[b,c]	1959–1995	19	135	0.28	0.04	1
	Dungeness[b]	1959–1995	19	88	0.43	–0.30	1
Fraser River (FR)	Total[b]	1957–1995	20	10 815	0.64	–0.24	2, 3
Mainland B.C. (MBC)	Statistical Areas 12, 13, 15, 16[d]	1954–1994	21	2 439	0.56	0.14	4, 5
Central B.C. (CBC)	Statistical Area 10	1950–1995	46	38	0.53	–0.10	6, 7
	Statistical Area 9	1950–1996	47	259	0.55	–0.26	6, 7
	Statistical Area 8	1950–1996	47	2 704	0.46	–0.21	6, 7
Northern B.C. (NBC)	Statistical Area 6	1950–1995	46	2 022	0.57	–0.02	6, 7
	Statistical Area 2E	1950–1995	46	443	0.22	0.01	6, 7
Southeast Alaska (SEA)	Southern (Districts 101–108)	1960–1996	37	30 826	0.56	0.15	8
	Northern inside (109–112, 114, 115)	1960–1996	37	12 263	0.46	0.40*	8
	Northern outside (113)	1960–1996	37	3 167	0.21	0.33*	8
Yakutat (YAK)	Situk River	1962–1990	25	204	0.10	0.00	8, 9
	Humpy Creek	1962–1992	22	76	0.28	–0.08	8, 9
Prince William Sound (PWS)	Eastern D	1967–1996	30	3 475	0.72	0.25	10
	Montague D	1971–1996	26	302	0.20	0.11	10
	Southeastern D	1967–1996	30	979	0.43	0.12	10
Lower Cook Inlet (CK)	Southern D[e]	1960–1996	37	219	0.35	0.12	11
	Outer D[f]	1960–1996	37	367	0.48	0.22	11
	Kamishak D[g]	1960–1996	34	190	0.19	0.06	11
Kodiak Island (KOD)	Afognak D	1980–1996	17	1 337	0.60	–0.21	12
	Westside D	1980–1996	17	7 602	0.64	–0.46	12
	Alitak D	1980–1996	17	2 189	0.58	–0.05	12
	Eastside–Northend D	1980–1996	17	2 856	0.52	–0.16	12
	Mainland D	1980–1996	17	1 390	0.42	0.12	12
	Across Districts (extra years)	1962–1996	35	13 330	0.68	0.15	12
Chignik (CHG)	Chignik Bay D	1962–1995	31	115	0.80	–0.12	13, 14
	Central D	1962–1995	34	245	0.40	0.21	13, 14
	Eastern D	1962–1995	34	575	0.24	0.12	13, 14
	Western D	1962–1995	34	458	0.58	0.22	13, 14
	Perryville D	1962–1995	34	364	0.47	0.11	13, 14
Alaska Peninsula (PEN)	Northwestern D	1962–1996	35	60	0.32	0.14	13, 15
	Southeast D and South-central D	1962–1996	35	4 427	0.58	0.50*	13, 16
	Southwest D and Unimak D	1962–1996	35	1 842	0.51	0.50*	13, 16
Bristol Bay (BB)	Nushagak D[h]	1960–1996	17	2 673	0.49	0.08	17
Norton Sound (NS)	Nome	1978–1995	17	311	0.12	0.04	18, 19
	Golovin	1968–1995	18	318	0.29	–0.19	18, 19
	Moses Point and Norton Bay	1963–1994	24	281	0.13	0.06	18, 19
	Unakleet	1962–1995	23	144	0.54	–0.13	18, 19

Note: Also shown is the "Across Districts" data set for the Kodiak Island region. *N* is the number of brood years available, *R* is the average recruitment (thousands), *H* is the average harvest rate, and Lag1 is the lag-1 autocorrelation in the time series of residuals from the Beverton–Holt model. An asterisk denotes significant lag-1 autocorrelation ($p < 0.05$).

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[b]Data were only available for odd years (e.g., brood years 1959, 1961,...,1995) because few if any pink salmon spawn in even years.

[c]Sum of Dosewallips, Duckabush, and Hamma Hamma data sets.

[d]Only even-year data were used for the Mainland B.C. data set because catches in most odd years were confounded by catch of Fraser River pink salmon.

[e]Sum of Humpy Creek, Port Graham, and Seldovia Bay data sets.

[f]Sum of Port Chatham, Port Dick, Rocky River, and Windy Creek data sets.

[g]Sum of Brown's Peak Creek, Bruin River, and Sunday Creek data sets.

[h]Data were only available for even years because few if any pink salmon spawn in odd years.

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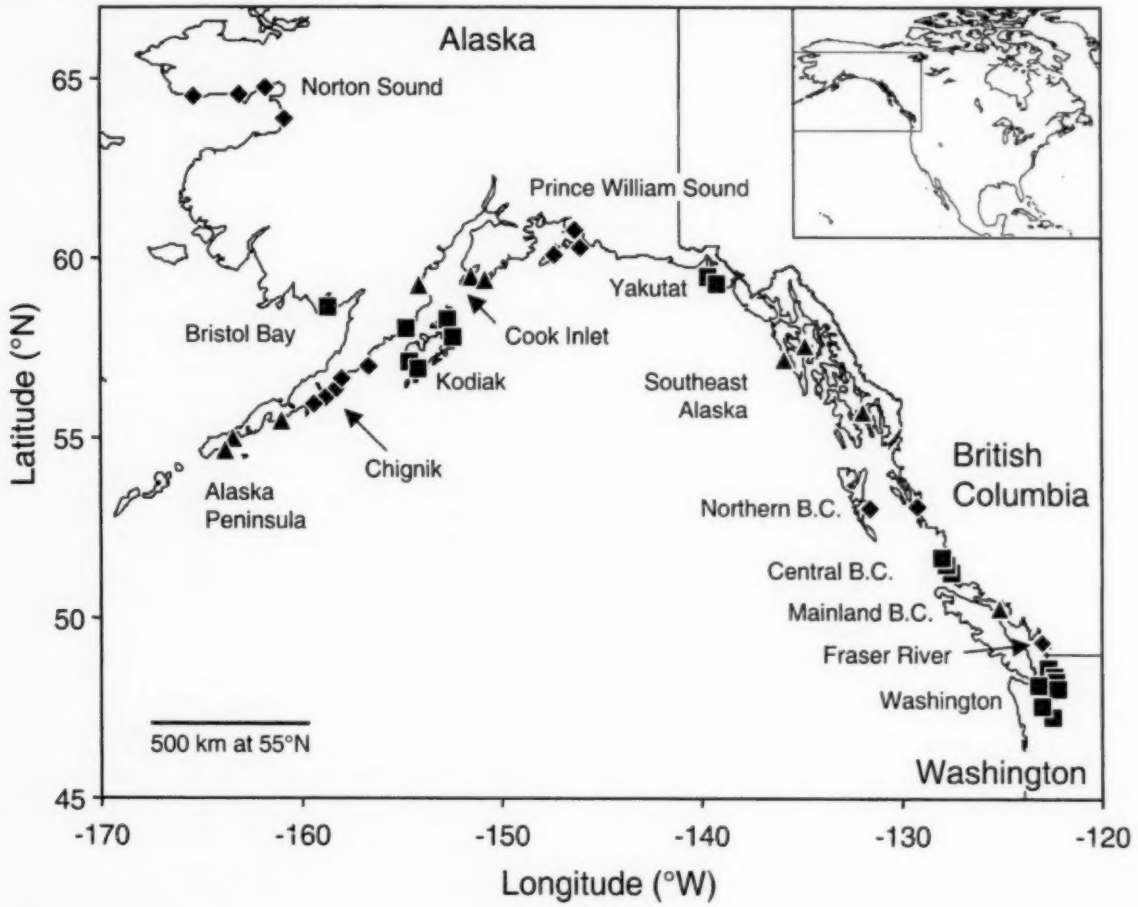
Fig. 1. Distribution of ocean-entry locations for 43 wild stocks or stock groups of pink salmon with stock–recruit data. Stocks are organized into 14 management areas or regions from south to north: Washington (squares), Fraser River (diamond), Mainland B.C. (triangle), Central B.C. (squares), Northern B.C. (diamonds), Southeast Alaska (triangles), Yakutat (squares), Prince William Sound (diamonds), Lower Cook Inlet (triangles), Kodiak Island (squares), Chignik (diamonds), Alaska Peninsula (triangles), Bristol Bay (square), and Norton Sound (diamonds).



dex to better depict the "signal," or variation in survival rate, shared among them (e.g., Thompson and Page 1989). This was done by first standardizing each stock-specific SR index to have unit variance (so that each index had equal weighting) and then averaging them for each year. As noted above, in these analyses, we used the Across Districts SR index for Kodiak Island instead of the aggregated index of the five separate districts to provide a much longer time series for this region (Table 1); over the period 1980–1996, these two indices were highly correlated ($r = 0.94$). In addition, the single SR indices for Fraser River, Mainland B.C., and Bristol Bay represented those respective regions. We then repeated the correlation analysis using these 14 region-specific SR indices to further examine patterns of covariation between regions.

To further characterize spatial patterns of covariation among the 43 stock-specific and 14 region-specific SR indices, we examined the rate of decay in correlation as a function of distance. Specifically, the correlation coefficient between the SR indices of two stocks was plotted against the great circle distance between their points of ocean entry. For data sets representing district or area totals, we used the center of that geographical area to calculate distances. To describe the relationship between correlation and distance, we fit an exponential model or "covariance function" to the data (Myers et al. 1997). Model parameters consist of the Y-intercept (constrained to a maximum of 1), corresponding to the correlation at zero distance, and the e-folding scale, corresponding to the distance at which the correlation declines to 37% (i.e., $e^{-1} \times 100\%$) of its value at zero distance. Parameters were fit using nonlinear least squares, with each correlation weighted by its sample size. Because the pairwise correlations are not independent, classical confidence intervals are not valid. Thus, we used a bootstrap procedure to obtain approximate confidence bands for the exponential covariance function and its parameters based on 2000 bootstrap replicates (Bjornstad et al. 1999). In this procedure, the 43 SR indices were resampled with replacement prior to fitting the covariance function (Bjornstad et al. 1999). However, in simulations with small sample sizes (e.g., 15–50 years), we found that the bootstrap procedure of Bjornstad et al. (1999) produced confidence bands that were too narrow because it does not account for imprecision in estimated pairwise correlations. We therefore modified the procedure by first resampling with replacement the years for which data were available across SR indices and then resampling SR indices as before. Simulations

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Table 2. Summary of data sets for nine wild (W) and 13 hatchery (H) pink salmon stocks with juvenile data used to compute times series of freshwater (F) and marine (M) survival rate indices.

Region	Stock	Brood years	*N*		Lag1		Source[a]
			F	M	F	M	
Fraser River (FR)	Total W[b]	1961–1995	19	18	–0.04	–0.36	1, 2
Mainland B.C. (MBC)	Quinsam H (A)[c]	1979–1992		14		0.11	3
	Quinsam H (B)[d]	1979–1991		13		0.50	3
	Puntledge H[c]	1979–1992		13		0.22	3
Central B.C. (CBC)	Atnarko River W[e]	1974–1996	23	21	0.56*	–0.28	4
Southeast Alaska (SEA)	Auke Creek W[f]	1971–1996	27		0.17		5
	Sashin Creek W	1950–1997	31		–0.37*		6
	Kowee Creek H	1977–1986		10		–0.24	7
	Sheep Creek H	1980–1992		12		0.05	7
	Gastineau H	1987–1996		10		–0.31	7
	Sheldon Jackson H	1977–1996		20		0.41	8
Prince William Sound (PWS)	Total W[e]	1960–1996	37	37	0.07	–0.13	9
	Koenig H	1975–1996		22		0.19	9
	Noerenberg H	1985–1996		12		0.18	9
	Cannery H	1978–1996		19		–0.01	9
	Solomon H	1981–1996		16		–0.24	9
Lower Cook Inlet (CK)	Tutka Bay H	1977–1996		20		–0.02	10
Kodiak Island (KOD)	Afognak W[e]	1978–1996	17	19	–0.03	–0.10	11
	Westside W[e]	1978–1996	17	19	–0.28	–0.51*	11
	Alitak W[e]	1978–1996	17	19	0.04	–0.26	11
	East–Northside W[e]	1978–1996	17	19	0.28	–0.46*	11
	Kitoi Bay H	1972–1996		24		–0.19	12

Note: *N* is the total number of brood years available and Lag1 is the lag-1 autocorrelation in the time series of residuals from the Ricker (for F) and Beverton–Holt (for M) models. An asterisk denotes significant lag-1 autocorrelation ($p < 0.05$).

[a]1. Al Cass, Canadian Department of Fisheries and Oceans (DFO), Nanaimo, B.C. (personal communication); 2. Jim Woodey, Pacific Salmon Commission, Vancouver, B.C. (personal communication); 3. Don Bailey, DFO, Vancouver, B.C. (personal communication); 4. Russ Hilland, DFO, Bella Coola, B.C. (personal communication); 5. Jerry Taylor, National Marine Fisheries Service (NMFS), Juneau, Alaska (personal communication); 6. Ron Heinz, NMFS, Juneau, Alaska (personal communication); 7. Rick Focht, Douglas Island Pink and Chum Corporation, Juneau, Alaska, (personal communication); 8. Bill Coltharp, Sheldon Jackson College Hatchery, Sitka, Alaska (personal communication); 9. Mark Willette, Alaska Department of Fish and Game (ADFG), Cordova, Alaska (personal communication); 10. George Bowden, Cook Inlet Aquaculture Association, Kenai, Alaska (personal communication); 11. Kevin Brennan, ADFG, Kodiak, Alaska (personal communication); 12. Andy Hall, Kodiak Regional Aquaculture Association, Kitoi Bay, Alaska (personal communication).

[b]Fry abundance estimates were derived from traps in the lower Fraser River.

[c]Releases of fed fry.

[d]Releases of unfed fry.

[e]Fry abundance measured as densities (e.g., number per square metre) of preemergent alevins or fry in gravel spawning beds.

[f]Fry abundance measured as densities of preemergent fry for 1970–1979, after which fence counts of migrating fry were used.

using this procedure resulted in reasonable, although slightly conservative, confidence intervals (e.g., 95% confidence intervals contained the true parameter value 97% of the time).

Finally, to examine spatial patterns of covariation in survival rates for a given life stage, we computed correlations among the nine freshwater survival rate indices and among the 20 marine survival rate indices. For these analyses, correlations were computed only if two data sets had 10 or more years in common. Again, we used standard significance tests because there was little autocorrelation in either freshwater or marine indices (Table 2).

Causes of patterns of covariation: freshwater or marine processes?

We explored the extent to which each life stage contributed to the overall covariation among SR indices using two approaches. First, for each of seven wild stocks, we compared correlations between the SR index and the freshwater and marine indices to see which life stage best accounted for variability in overall survival rate. Second, we compared correlations between a given region's marine and freshwater indices and the SR indices of those regions for which there was evidence of positive between-region covariation among SR indices. For these analyses, we used regional aggregated SR indices, as well as aggregated marine and freshwater indices for the Kodiak region (wild stocks only), to best depict the variability shared by each region's stock-specific indices.

Sensitivity analyses

We examined the sensitivity of patterns of covariation among SR, freshwater, and marine indices to the choice of stock–recruitment model (Beverton–Holt or Ricker) used to compute each index of survival rate. In addition, we tested the assumption of normality for survival rate indices using the test procedure of Shapiro and Wilk (1965). We then examined the sensitivity of our results to outliers.

Randomization tests

We used randomization tests (Manly 1997) to evaluate the statistical significance of average correlations both within and between regions with replicate SR indices. Such tests provide high statistical power because inferences are based on multiple (i.e., replicate) correlation coefficients. Moreover, for the types of hypotheses examined here, randomization tests have been shown to have greater statistical power than other approaches such as Bartlett's sphericity

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test (e.g., Thompson and Page 1989). These tests also addressed the problem of missing data points.

Specifically, we used randomization tests to examine three hypotheses regarding spatial patterns of covariation. First, for each region with more than two SR indices, we tested the null hypothesis that the average correlation ($\bar{r}$) among them was zero (i.e., H_0: $\bar{r} = 0$, no within-region covariation). For example, if a region had four SR indices, we generated four normally distributed random time series of corresponding length (with appropriate missing data points) and averaged the pairwise correlations among them. This procedure was repeated 2000 times to generate a null distribution of 2000 replicates for $\bar{r}$. We then tabulated the proportion of the null distribution that was greater than the observed $\bar{r}$ to evaluate its statistical significance.

Next, we tested the hypothesis that the average correlation between the SR indices of two different regions ($\bar{r}_{12}$) was equal to zero (i.e., H_0: $\bar{r}_{12} = 0$, no between-region covariation). Because we found evidence of positive covariation among SR indices within each region, this lack of independence had to be accounted for when testing $\bar{r}_{12}$; otherwise, p values would be underestimated (i.e., Type I error rates would be greater than the specified alpha). Thus, to simulate the null distribution of $\bar{r}_{12}$, we first constructed a correlation matrix consisting of the observed within-region correlations and correlations of zero between regions (corresponding to the null hypothesis). Simulated time series were then drawn at random from a multivariate normal distribution with the above correlation structure using a method based on the Cholesky decomposition (Ripley 1987).

Finally, to identify groups of regions with similar levels of covariation in survival rates, we tested hypotheses that the SR indices of two regions came from the same "population" in terms of the magnitude of correlation among them. That is, we tested whether each average within-region correlation ($\bar{r}_{11}$ or $\bar{r}_{22}$) was equal to the average between-region correlation, $\bar{r}_{12}$ (i.e., H_0: $\bar{r}_{11} = \bar{r}_{12}$; $\bar{r}_{22} = \bar{r}_{12}$). These tests were only conducted for pairs of regions for which there was evidence of significant between-region covariation. The test statistics of interest were the observed differences in average correlations, $\bar{r}_{11} - \bar{r}_{12}$ and $\bar{r}_{22} - \bar{r}_{12}$. To simulate null distributions, we randomly generated time series from a multivariate normal distribution with the same correlation structure as observed among the SR indices of the two regions. We then randomly assigned the appropriate number of SR indices to each region (i.e., as though the SR indices came from the same "population") and computed the null test statistics for each of 2000 trials. We used one-tailed tests for the alternative hypotheses that $\bar{r}_{11} > \bar{r}_{12}$ and $\bar{r}_{22} > \bar{r}_{12}$ because it is biologically unreasonable that between-region correlations would be greater on average than within-region correlations.

Results and discussion

Patterns of covariation

We computed a total of 723 correlations among the 43 stock-specific spawner-to-recruit (SR) indices of survival rate. There were 495 positive correlations, of which 119 were significant ($p < 0.05$), while only four of the 228 negative correlations were significant. These correlations are summarized for each of the 14 regions in Fig. 2*a*.

First, there is strong evidence of positive within-region covariation across all regions for which replicate SR indices were available (shown in the diagonal of Fig. 2*a*). The within-region pairwise or average correlations ranged from 0.26 between the two Northern B.C. stocks to 0.71 among the three Alaska Peninsula stocks. In addition, the distributions of pairwise correlations among a given region's SR indices were reasonably consistent across replicate stocks. For example, the 21 correlations among the seven Washington SR indices ranged from 0.23 to 0.77 (Fig. 3*a*), while the 10 correlations for the Chignik region ranged from 0.27 to 0.67 (Fig. 3*b*). Note that averages of these two sets of correlations, which are 0.58 and 0.50, respectively, are shown for each region in Fig. 2*a*.

There is also strong evidence of positive between-region covariation among stock-specific SR indices for several groups of adjacent regions (i.e., those near the diagonal of the matrix in Fig. 2*a*; refer to Fig. 1). Significant covariation was found among the Mainland, Central, and Northern B.C. regions ($\bar{r}$ from 0.35 to 0.48), among the Yakutat, Prince William Sound, and Cook Inlet regions ($\bar{r}$ from 0.36 to 0.47), and among many combinations of regions extending from Cook Inlet to Bristol Bay ($\bar{r}$ from 0.25 to 0.56). However, there was little evidence of either positive or negative covariation between these groups of regions or between them and the remaining regions (Washington, Southeast Alaska, and Norton Sound) (Fig. 2*a*). Again, distributions of pairwise correlations were reasonably consistent across replicate stocks for comparisons between regions. For example, the 35 correlations between Washington and Chignik SR indices show a relatively even distribution of weak positive and negative correlations, ranging from –0.35 to 0.60 (Fig. 3*c*), which is reflected by their average of 0.03 (Washington versus Chignik) (Fig. 2*a*).

Pairwise correlations among the 14 region-specific SR indices (Fig. 4) showed patterns of between-region covariation similar to those for the 43 stock-specific indices, namely significant correlations only among certain nearby regions (Fig. 2*b*). Notably, correlations between regional aggregated SR indices were consistently larger than the corresponding average correlation among stock-specific indices for comparisons within each group of adjacent regions noted above. For example, the correlation between the Chignik and Alaska Peninsula aggregated indices was 0.81 (Fig. 2*b*), while the average correlation among their stock-specific SR indices was only 0.56 (Fig. 2*a*). In addition, using the longer Across Districts SR index for the Kodiak region also contributed to the much larger correlations between this region and the nearby Cook Inlet, Chignik, and Alaska Peninsula regions (Fig. 2*b*). As we found with stock-specific indices, region-specific SR indices showed no evidence of covariation among distant regions such as those of B.C. and central or western Alaska (Fig. 2*b*).

We summarized the dominant spatial patterns of covariation among stock-specific SR indices (Fig. 2*a*) for the Northeast Pacific by drawing boundaries around groups of stocks that showed significant positive covariation (Fig. 5). As described above, we used randomization tests to determine if within-region covariation was significantly greater than between-region covariation when there was evidence of the latter. For example, for all pairwise comparisons among the Mainland, Central, and Northern B.C. regions, average within-region correlations were not significantly greater than between-region averages. Consequently, they are enclosed in a single boundary (Fig. 5). In contrast, the inner boundary surrounding the Kodiak region reflects the significantly greater within-region covariation compared with its between-region covariation with either the Cook Inlet, Chignik, or Alaska

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Fig. 2. (*a*) Summary of pairwise correlations among the 43 stock-specific SR indices by region: Washington (WA), Fraser River (FR), Mainland B.C. (MBC), Central B.C. (CBC), Northern B.C. (NBC), Southeast Alaska (SEA), Yakutat (YAK), Prince William Sound (PWS), Lower Cook Inlet (CK), Kodiak Island (KOD), Chignik (CHG), Alaska Peninsula (PEN), Bristol Bay (BB), and Norton Sound (NS). The number of stock-specific SR indices for each region is shown in parentheses (e.g., WA (7)). Average correlations are shown for those regional comparisons that involve more than one correlation. Correlations in black boxes are significant ($p \leq 0.05$); shaded boxes indicate correlations for which $0.05 < p \leq 0.10$. (*b*) Pairwise correlations among the 14 region-specific SR indices. Aggregated indices (averages of stock-specific SR indices) were used for all regions except Fraser River, Mainland B.C., Kodiak Island, and Bristol Bay; see text for their derivation.

a)

	WA (7)	FR (1)	MBC (1)	CBC (3)	NBC (2)	SEA (3)	YAK (2)	PWS (3)	CK (3)	KOD (5)	CHG (5)	PEN (3)	BB (1)	NS (4)
WA (7)	0.58													
FR (1)	0.28													
MBC (1)														
CBC (3)	0.08	0.12	0.48	0.30										
NBC (2)	0.24	0.05	0.41	0.35	0.26									
SEA (3)	0.18	0.09	-0.21	0.02	-0.01	0.44								
YAK (2)				-0.03	0.08	0.07	0.54							
PWS (3)	0.23	0.26		-0.11	0.02	0.13	0.47	0.55						
CK (3)	0.04	0.33	0.15	0.01	0.06	0.04	0.39	0.36	0.50					
KOD (5)				-0.16	-0.27	-0.01		-0.14	0.27	0.56				
CHG (5)	0.03	-0.01	0.11	0.08	-0.06	0.10	-0.04	0.06	0.25	0.32	0.50			
PEN (3)	0.03	-0.02	-0.01	0.02	-0.14	0.23	0.04	0.12	0.27	0.36	0.56	0.71		
BB (1)			-0.13	0.03	-0.31	-0.01			0.18		0.51	0.47		
NS (4)				-0.06	-0.01	0.04	-0.09	0.04	0.03	-0.25	0.08	0.14		0.62

b)

	WA (7)	FR (1)	MBC (1)	CBC (3)	NBC (2)	SEA (3)	YAK (2)	PWS (3)	CK (3)	KOD (1)	CHG (5)	PEN (3)	BB (1)	NS (4)
WA (7)														
FR (1)	0.35													
MBC (1)														
CBC (3)	0.17	0.23	0.59											
NBC (2)	0.43	0.06	0.50	0.61										
SEA (3)	0.27	0.10	-0.29	0.03	-0.01									
YAK (2)				-0.10	0.04	0.01								
PWS (3)	0.41	0.41		-0.20	-0.03	0.19	0.47							
CK (3)	0.01	0.44	0.20	0.02	0.08	0.06	0.48	0.55						
KOD (1)	-0.22	-0.22	0.32	-0.02	-0.03	0.28	0.01	0.19	0.51					
CHG (5)	0.06	0.00	0.14	0.15	-0.09	0.15	-0.06	0.14	0.38	0.67				
PEN (3)	0.05	-0.02	-0.01	0.03	-0.20	0.33	0.01	0.20	0.35	0.72	0.81			
BB (1)			-0.13	0.08	-0.36	0.00			0.16	0.49	0.59	0.55		
NS (4)	0.14	0.30	-0.16	-0.03	0.05	0.11	0.14	-0.06	0.08	-0.08	0.14	0.20		

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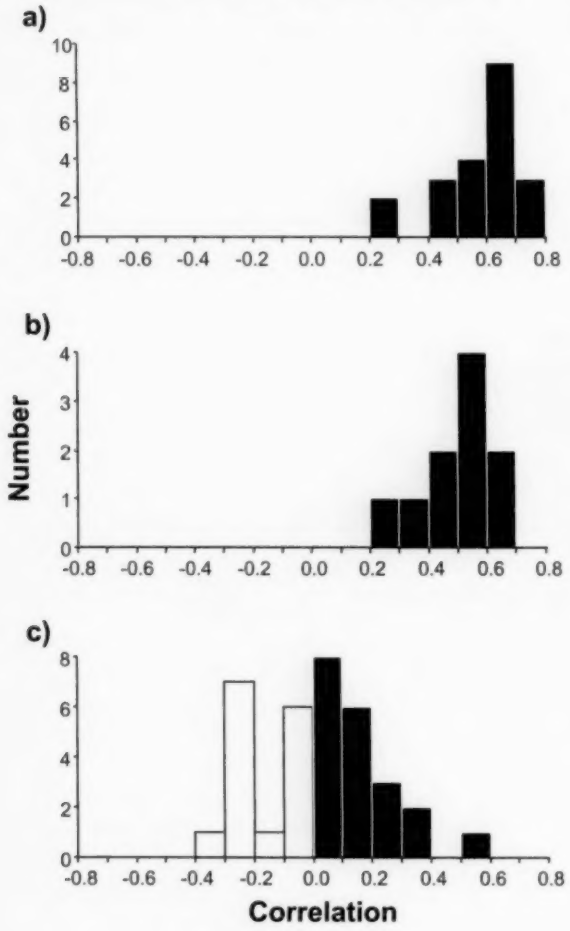
Fig. 3. Histograms of correlations between time series of stock-specific SR indices for comparisons (*a*) among the seven Washington pink stocks, (*b*) among the five Chignik stocks, and (*c*) between Washington and Chignik stocks. Open bars represent negative correlations; solid bars are positive correlations.



Peninsula region. Although none of the average correlations between Kodiak and Cook Inlet, Chignik, or Alaska Peninsula stock-specific SR indices was significant (Fig. 2*a*), we placed the boundary around these three regions and the Kodiak region because of the strong correlations observed among their region-specific SR indices ($p < 0.005$ for all three between-region comparisons with Kodiak) (Fig. 2*b*).

These patterns of covariation among SR indices suggest that key environmental (biological or physical) processes that influence SR survival rates of pink salmon stocks operate primarily at local or regional scales (e.g., across Mainland, Central, and Northern B.C.). Although we use the term "regional scale" as a general descriptor of these patterns, this term does not necessarily correspond to the "management regions" used in our analyses to define replicate stocks; rather, the patterns of covariation indicate a number of confined geographical areas over which significant shared influences of environmental processes are evident (Fig. 5). The tendency toward positive covariation among replicate stocks within a given management region is remarkably consistent across regions (Fig. 2), providing strong evidence of the dominant role of regional-scale processes. In addition, the clear definition of patterns of covariation between certain groups of adjacent regions lends further support to the geographically confined nature of shared environmental influences (Figs. 2 and 5). In contrast to this evidence for the importance of regional-scale processes, there is no evidence that broad-scale processes across the entire Northeast Pacific, for example, affected SR survival rates of pink salmon in similar ways over the period examined (Fig. 2).

In general, the influences of shared environmental effects on SR survival rates appear to decline rapidly as the distance between two stocks increases (Fig. 6*a*). As suggested by the exponential covariance function, the correlation among SR indices declines from roughly 0.6 for nearby stocks (e.g., separated by <100 km) to near zero for stocks separated by 1000 km or more. The estimate of the *e*-folding scale was 431 km, with a 95% confidence interval of 286–708 km. Although the *Y*-intercept was significantly less than 1 ($p < 0.001$), we also computed the *e*-folding scale with the *Y*-intercept set to 1 as in Myers et al. (1997). This reduced our estimate of the *e*-folding scale to 260 km, whereas Myers et al. (1997) reported an estimate of 100 km for SR survival rates of 32 pink salmon stocks across both the Northeast and Northwest Pacific. Our larger estimate is likely more accurate for pink salmon stocks in the Northeast Pacific because our data set contains more stocks, longer time series, and a much more complete geographical distribution of stocks. A similar pattern of decline exists for correlations among the 14 region-specific indices, except that the magnitude of correlation is greater at distances less than 1000 km (Fig. 6*b*). The estimate of the *e*-folding scale was 425 km, which is nearly identical to that for the 43 stock-specific indices (Fig. 6). In addition, the fits of the exponential model (Fig. 6) were nearly identical to those obtained using a robust nonparametric covariance function (Bjornstad et al. 1999), indicating that the exponential model provided a good depiction of the relationships between correlation and distance. In general, these results suggest that the coherence of key physical or biological factors influencing survival rates should show a similar pattern of decline in correlation with distance.

Patterns of covariation among freshwater and among marine indices of survival rate also indicate that the shared influence of environmental processes is restricted to local or regional scales. For the nine freshwater indices, there was positive covariation only within the Kodiak region. The six correlations among Kodiak freshwater indices ranged from 0.26 to 0.64 ($\bar{r} = 0.47$, $p < 0.01$), with four correlations being significant. In contrast, the 21 other correlations among Kodiak, Prince William Sound, Southeast Alaska, Central B.C., and Fraser River freshwater indices ranged from –0.32 to 0.25 ($\bar{r} = 0.02$), with no significant values.

Among the 20 indices of marine survival rate, we found significant positive covariation within regions and between certain adjacent regions (Fig. 7). Average within-region correlations ranged from 0.33 for Southeast Alaska to 0.72 for Mainland B.C. There was also significant positive covariation among marine indices of Southeast Alaska and

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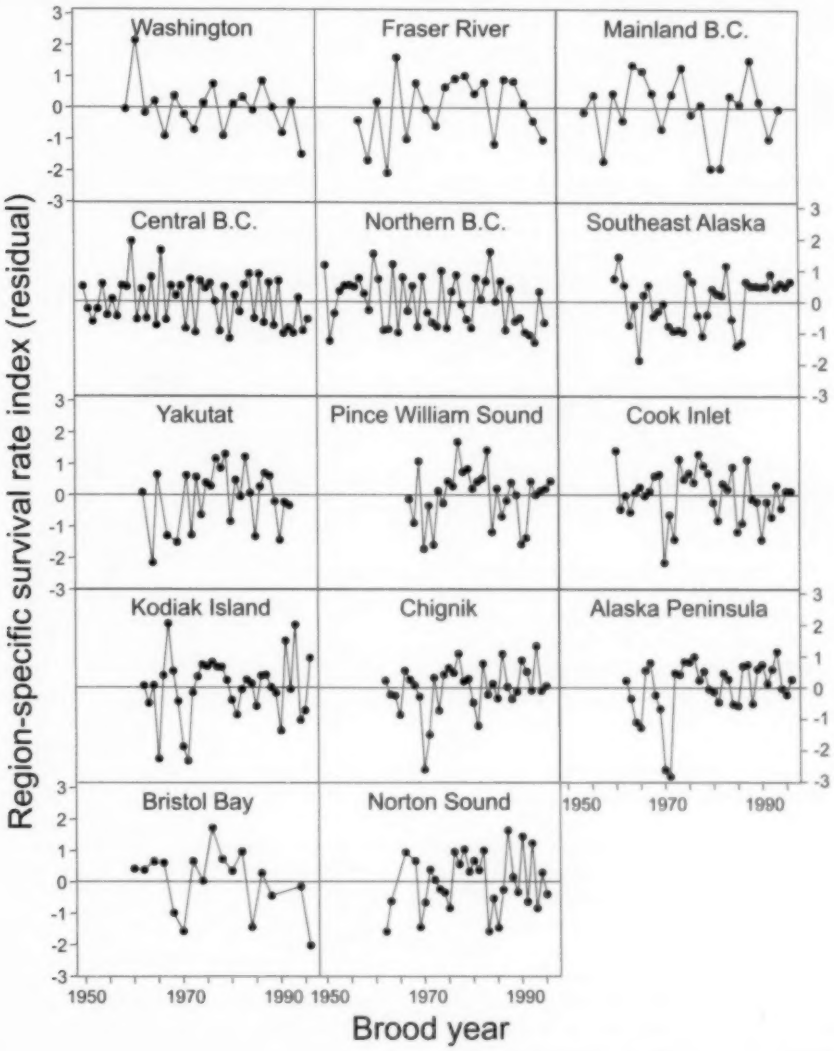
Fig. 4. Time series of the 14 region-specific SR indices. Aggregated indices (averages of stock-specific SR indices) are shown for all regions except Fraser River, Mainland B.C., Kodiak Island, and Bristol Bay, which each contained only one stock.



Prince William Sound ($\bar{r}$ = 0.38) that was not evident among SR indices (Fig. 2); however, the correlations among marine indices should be interpreted more cautiously because they are based on much smaller sample sizes (average n of 13) than for SR indices (average n of 29). Positive covariation was also evident among the marine index for Cook Inlet (Tutka Bay Hatchery) and the five indices of the adjacent Kodiak region ($\bar{r}$ = 0.40). As with SR indices, there was little evidence of either positive or negative covariation between distant regions, except perhaps for a tendency toward negative correlations between B.C. indices and those of the Cook Inlet and Kodiak regions in Alaska (Fig. 7). Our results extend those of Blackbourn (1998) who examined correlations among a different index of marine survival rate (time series of recruits per fry) for six wild and nine hatchery stocks from B.C. and Alaska. He found strong evidence of positive covariation only within the Prince William Sound region, whereas our results demonstrate positive covariation within several regions as well as between certain adjacent regions (Fig. 7).

Causes of patterns of covariation: freshwater or marine processes?

The patterns of covariation in SR indices could arise from regional covariation in freshwater or marine survival rates, or both. The only region for which we had replicate stocks with both freshwater and marine indices was the Kodiak region. For the four Kodiak wild stocks with fry data, the average correlation among their SR indices was 0.63. As noted above, there was also significant positive covariation among these four stocks for both freshwater indices ($\bar{r}$ = 0.47) and marine indices ($\bar{r}$ = 0.39), indicating that shared environ-

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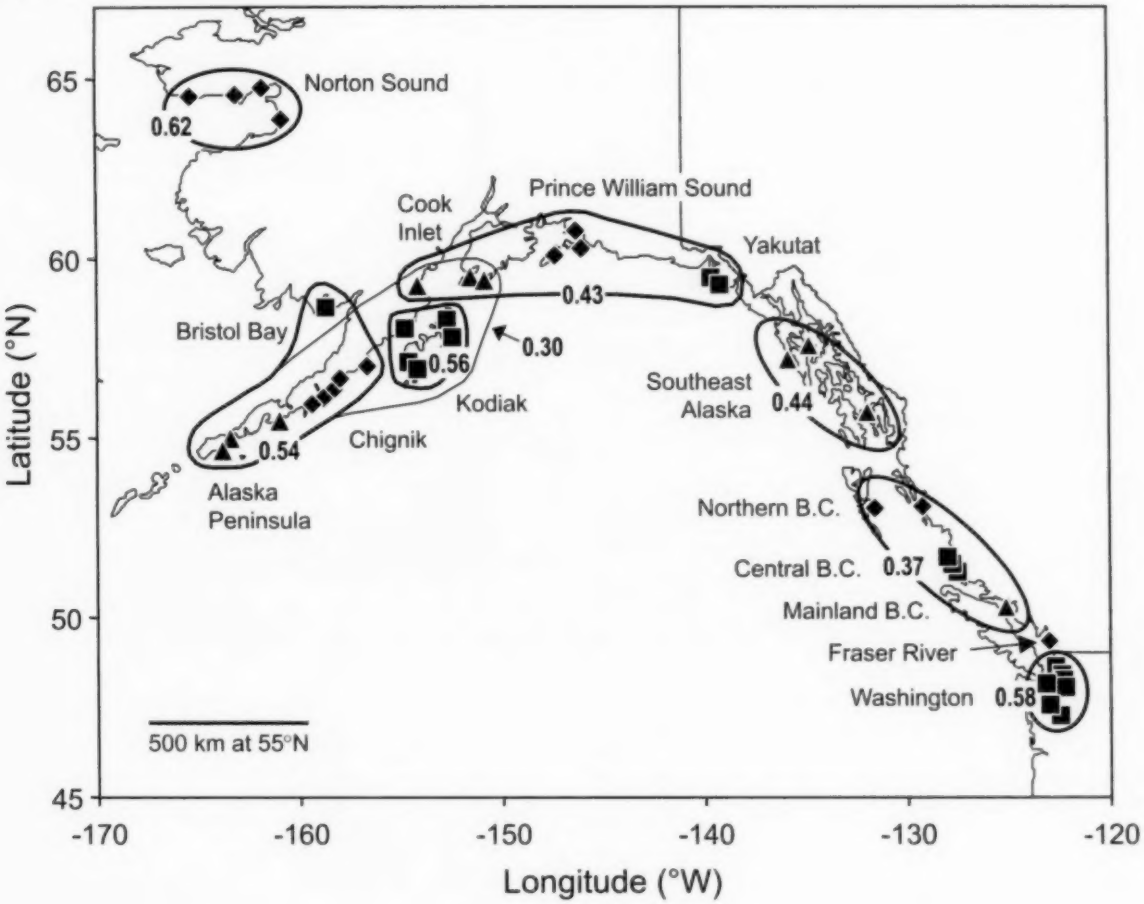
Fig. 5. Summary of patterns of covariation among the 43 SR indices by region. Boundaries denote individual regions or groups of adjacent regions for which there was evidence of significant ($p < 0.05$) positive covariation. Values on each boundary represent the average correlation for a given set of comparisons among SR indices; see text for details. Symbols are used to distinguish stocks by management region as in Fig. 1.



mental influences were important during both life stages. However, two lines of evidence suggest that marine processes play a dominant role in determining regional-scale covariation among SR indices.

First, for the seven wild stocks with freshwater and marine indices, correlations of these indices with each stock's SR index were consistently larger for the marine index ($\bar{r} = 0.82$) than for the freshwater index ($\bar{r} = 0.43$) (Table 3). Interestingly, average correlations were very similar for each life stage before within-stock density-dependent effects were removed (i.e., correlations among time series of $\log_e$(recruits per spawner), $\log_e$(fry per spawner), and $\log_e$(recruits per fry)) (Table 3). By comparison, Bradford (1995) found that across five data sets (including the Fraser River stock used here), variability in survival of pink salmon during the freshwater ($\log_e$(fry per egg)) and marine ($\log_e$(recruits per fry)) life stages accounted for 64 and 36%, respectively, of the variability in overall survival rate ($\log_e$(recruits per spawner)). However, we found that removing possible density-dependent effects of abundance on survival rate (i.e., by using residuals from stock–recruitment models as indices of survival rate) reveals a much greater tendency for marine survival rates to reflect patterns of variability in the overall survival rate that are unrelated to stock abundance. With density-dependent effects removed, the proportion of variation shared between marine indices and SR indices is 67% on average (i.e., $\bar{r}^2 \times 100$) across the seven wild stocks but only 18% for freshwater indices (from $\bar{r} = 0.82$ and 0.43 in Table 3). Thus, we might expect that covariation among these stocks' SR indices and those of other stocks is determined largely by processes influencing their marine life stage.

Indeed, this hypothesis is supported by correlations between freshwater or marine indices for wild stocks and selected region-specific SR indices (Table 4). For this second set of analyses, we limited our comparisons to those regions for which there was evidence of between-region covariation among SR indices (Fig. 2). For seven of the eight comparisons, SR indices were more highly correlated with marine indices than with freshwater indices (Table 4). The average correlation for marine indices was 0.50 with five significant

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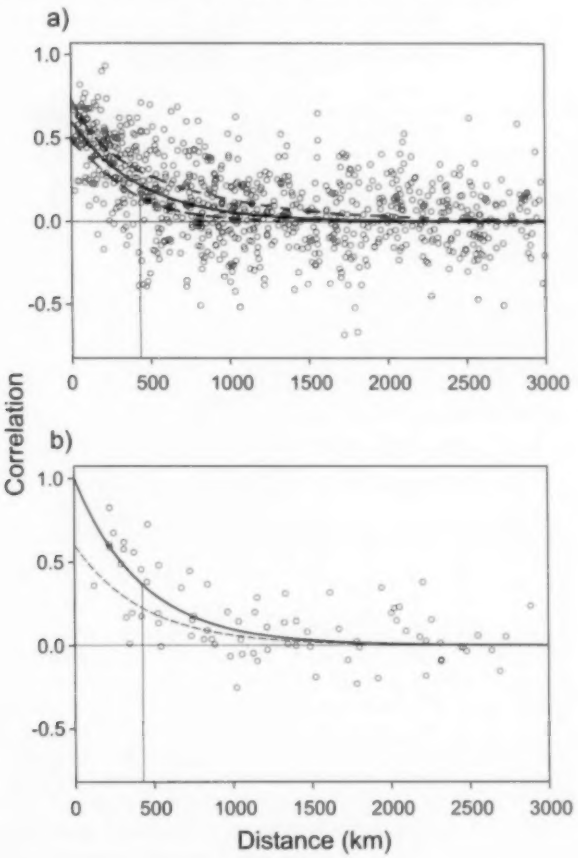
Fig. 6. (*a*) Plot of the magnitude of each pairwise correlation among the 43 stock-specific SR indices as a function of the distance between the points of ocean entry for each pair of stocks. The solid line represents the fit of the exponential model to the data, with a 95% confidence interval (broken lines). The vertical line marks the *e*-folding scale. (*b*) Fit of the exponential model (solid line) to correlations among the 14 region-specific SR indices as a function of distance. The initial estimate of the *Y*-intercept was slightly greater than 1; thus, this parameter was constrained to 1. For comparison, the exponential covariance function for the 43 stock-specific SR indices in Fig. 6*a* is also shown (broken line).



correlations, whereas the average for freshwater indices was only 0.14 with just one significant correlation.

These analyses suggest that regional-scale marine processes are the primary source of covariation among SR indices, although our inferences are limited to a few stocks. Mark–recapture experiments demonstrate that during their first few months at sea, pink salmon fry originating within the same region have similar migratory habits and therefore occupy the same coastal waters with distributions that remain generally distinct from pink salmon fry of other regions (Hartt 1980; Farley and Munk 1997). In addition, mortality rates are very high during this period and therefore can drive patterns of interannual variability in overall marine survival rates (Parker 1968; Ricker 1976). Thus, it is plausible that much of the covariation observed among SR indices arises from regional-scale similarities in coastal ecosystems and weather patterns that affect biological and physical conditions (e.g., temperature, food supply, competition, and predator abundances) and hence growth and mortality of fry during early marine life. However, our results must be interpreted cautiously because the marine indices for most wild stocks (except Fraser River) were derived using preemergent fry data and thus contain a component of late freshwater survival. In addition, it is also possible for covariation in marine survival rates of nearby stocks to arise from similarities in freshwater conditions such as stream temperatures, which can influence the timing of fry emigration to coastal waters and hence the marine conditions that they encounter (Cooney et al. 1995; Henderson et al. 1995). Covariation in freshwater survival rates of nearby stocks likely arises from regional-scale similarities in stream temperatures and flow rates, for example, which can be important determinants of egg and alevin survival rates (Wickett 1958; McNeil 1964).

Sensitivity analyses

The choice of stock–recruitment model had very little influence on the patterns of covariation among SR, freshwater, and marine indices of survival rate (Figs. 2–7; Tables 3 and 4). For a given stock and life stage, indices derived from the Beverton–Holt and Ricker models were typically highly correlated. Across stocks, the average correlations between the Beverton–Holt- and Ricker-based indices were 0.96, 0.89, and 0.95 for SR, freshwater, and marine indices, respectively.

However, results for a number of comparisons among SR indices were sensitive to outliers. Of the 43 SR indices, six showed significant ($p < 0.05$) departures from normality due to one or two outliers. Removing these outliers had little influence on correlations except for three data sets: Central District (Chignik) and the two Southern District data sets for Alaska Peninsula. More generally, there was a consistent pattern of negative outliers across the eight Chignik and Alaska Peninsula SR indices in brood years 1970 and 1971, which is evident in the region-specific SR time series (Fig. 4). In fact, of the 1214 total data points among all SR indices, 14 had absolute values greater than 2.5 SD units, and nine of these occurred among the Chignik and Alaska Peninsula stocks in those two brood years.

When brood years 1970 and 1971 were removed from the eight Chignik and Alaska Peninsula indices, average correlations decreased consistently from their values in Fig. 2*a* by 0.19–0.30 for comparisons within each region, between these two regions, and between each region and the Cook Inlet and Bristol Bay regions. For all four comparisons with Cook Inlet and Bristol Bay, the average correlations became weak (ranging from 0.05 to 0.28) and no longer significant ($p > 0.10$). Likewise, correlations between region-specific SR indices (Fig. 2*b*) decreased by 0.13–0.15 for the three comparisons among the Chignik, Alaska Peninsula, and Kodiak indices and by 0.26–0.31 for the four comparisons with the Cook Inlet and Bristol Bay indices. Again, none of the latter four comparisons remained significant.

Thus, it appears that much of the covariation observed between the complete time series of SR indices of the Chignik and Alaska Peninsula regions and those of the Cook Inlet and Bristol Bay regions was due to a common pattern of extremely low survival rates of central and western

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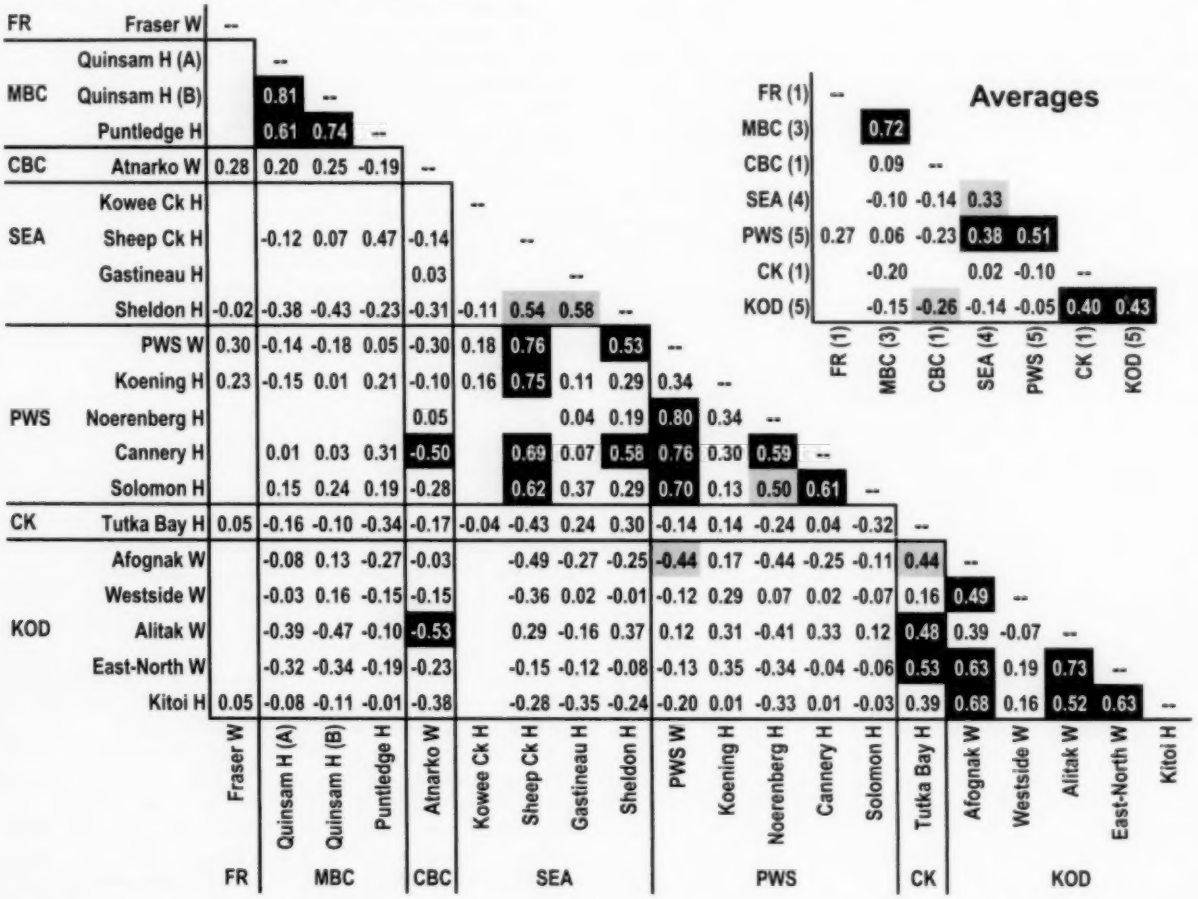
Fig. 7. Pairwise correlations among the 20 indices of marine survival rate for seven regions: Fraser River (FR), Mainland B.C. (MBC), Central B.C. (CBC), Southeast Alaska (SEA), Prince William Sound (PWS), Lower Cook Inlet (CK), and Kodiak Island (KOD). Average correlations for each regional comparison are shown in the inset. Correlations in black boxes are significant ($p \leq 0.05$); shaded boxes indicate correlations for which $0.05 < p \leq 0.10$.



Alaska pink salmon in the 1970–1971 brood years. Notably, air and sea surface temperatures were exceptionally low in the winters of both 1970–1971 and 1971–1972 (e.g., Royer 1993) and may well have produced broad-scale conditions unfavorable to either freshwater or marine survival rates, or both. Across the remaining brood years, environmental processes influencing survival rates of Chignik, Alaska Peninsula, and Kodiak pink salmon appear to be quite distinct from those influencing pink salmon of either the Cook Inlet or Bristol Bay region.

In addition, one of the 20 marine indices (Cannery) and two of the nine freshwater indices (Sashin and Afognak) also showed significant departures from normality. However, removing outliers from these indices or large deviates (e.g., >2.5 SD units) from other marine or freshwater indices had little effect on correlations involving these stocks.

Limitations

Over the period examined (roughly 1960–1995 for most data sets), we found no evidence of broad-scale covariation in survival rates of pink salmon from distant regions in Washington, B.C., and Alaska (Figs. 2, 5, 6, and 7). We also found little evidence of positive autocorrelation in the SR indices (Table 1), suggesting that variation in survival rates occurred mostly at short time scales (i.e., rapid year-to-year changes) (Fig. 4). In contrast, other investigators reported abrupt and persistent (long-term) increases in abundance of pink salmon and other salmon species throughout much of the Northeast Pacific beginning in the mid-1970s and speculated that the increases in abundance were due to increased productivity (survival rates) associated with concurrent shifts in climatic, physical, and biological conditions in the Northeast Pacific (e.g., Beamish and Bouillon 1993; Francis et al. 1998). However, their inferences were based largely on trends in total catch across large geographical areas of B.C. and Alaska. Although this approach provides for lengthy data series (e.g., from the early 1900s to the present), it precludes comparisons among separate stocks or stock groups within the various regions of B.C. and Alaska. More importantly, catch or total recruitment data may be poor surrogate measures of survival rate because they do not account for changes in spawner abundance or harvest rate over time

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Table 3. Correlations among two measures of freshwater and marine survival rate for a given wild pink salmon stock and the corresponding measure of overall spawner-to-recruit survival rate for that stock.

Stock	Years of data	Correlation between $\log_e$(recruits per spawner) and		Correlation between the SR index and	
		$\log_e$(fry per spawner)	$\log_e$(recruits per fry)	freshwater index	marine index
Fraser River (FR)	18	0.74	0.56	0.47	0.81
Atnarko (Central B.C. (CBC))	22	0.66	0.42	0.57	0.80
Prince William Sound (PWS)	35	0.50	0.83	0.47	0.87
Afognak (Kodiak (KOD))	17	0.67	0.57	0.58	0.79
Westside (KOD)	17	0.59	0.41	0.13	0.81
Alitak (KOD)	17	0.63	0.55	0.33	0.79
Eastside–Northend (KOD)	17	0.43	0.68	0.44	0.85
Average		0.60	0.57	0.43	0.82

Table 4. Correlations among the freshwater and marine indices of wild pink salmon stocks with fry data and selected region-specific SR indices.

Stock with fry data	Region-specific SR index	Years of data	Correlation between the region-specific SR index and	
			freshwater index	marine index
Atnarko (Central B.C. (CBC))	Mainland B.C. (MBC)	11	0.53	0.66*
Atnarko (CBC)	Central B.C. (CBC)	22	–0.15	0.58*
Atnarko (CBC)	Northern B.C. (NBC)	22	0.12	0.63*
Prince William Sound (PWS)	Yakutat (YAK)	27	–0.20	0.38
Prince William Sound (PWS)	Cook Inlet (CK)	37	0.43*	0.29
Kodiak (KOD) (aggregated)	Cook Inlet (CK)	17	–0.01	0.44
Kodiak (KOD) (aggregated)	Chignik (CHG)	17	0.19	0.56*
Kodiak (KOD) (aggregated)	Alaska Peninsula (PEN)	17	0.19	0.50*
Average			0.14	0.50

Note: For this analysis, the region-specific SR index for CBC was computed by averaging across the Area 9 and Area 10 SR indices only because the Area 8 SR index is composed of primarily Atnarko pink salmon. An asterisk denotes significant correlations ($p < 0.05$).

(e.g., Peterman et al. 1998). For many of the stocks considered here (e.g., Fraser River, Southeast Alaska, Prince William Sound, Kodiak Island, Chignik, and Alaska Peninsula stocks), catch and total recruitment increased dramatically beginning in the mid-1970s, but spawning escapements also increased. The importance of spawning escapement in determining subsequent recruitment cannot be ignored. Using survival rate indices such as those computed here (i.e., residuals from stock–recruitment models) eliminates potential confounding effects of changes in harvest rate and spawner abundance (Thompson and Page 1989; Myers et al. 1997; Botsford and Paulsen 2000).

However, a potential problem with our approach is that fitting stock–recruitment models may remove evidence of slowly changing patterns of productivity (i.e., persistent decadal-scale or long-term trends in survival rates) (Walters 1990; Myers et al. 1997). For data sets with periods of both increased recruitment and increased escapement after the mid-1970s, a stock–recruitment model will, in general, attribute a portion of these large recruitments to increases in spawner abundance (i.e., an apparent lack of density dependence). Thus, the key question is to what extent were the large and persistent increases in recruitments of certain B.C. and Alaska pink salmon stocks due to persistent increases in productivity (i.e., survival rates at a given spawner abundance) versus increases in spawner abundance? One approach to dealing with this problem is to formulate stock–recruitment models with time-varying parameters in an attempt to explicitly model persistent changes in productivity (e.g., Peterman et al. 2000). This topic warrants further investigation but is beyond the scope of this paper. Nevertheless, even if our approach to computing survival rate indices has removed some component of variability that was shared by many regions in the Northeast Pacific, it is clear that regional-scale processes predominate. For example, correlations among the 14 region-specific indices demonstrate that covariation between nearby regions is much greater than between distant regions (Figs. 2*b* and 6*b*).

Several other factors can create spurious covariation among indices of survival rate or can mask real patterns of covariation. Depending on the circumstance, both problems can arise from either errors in catch allocation or straying of fish. However, most stocks used in our analyses represent large groups of adjacent populations for which catch allocation errors or straying rates between stocks are likely quite limited. Although the data sets used in this analysis contain various degrees of measurement error, they still reveal consistent evidence of regional-scale covariation that presumably reflects the spatial scale of environmentally driven variability in survival rate shared among stocks. Because measurement error applies to all stocks regardless of the distance between them, such error cannot account for the large

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differences observed between the magnitude of regional-scale versus broad-scale covariation (Figs. 2 and 6).

Conclusions

Our analyses demonstrate that survival rates of pink salmon stocks in the Northeast Pacific are influenced by processes that operate at local and regional spatial scales, primarily at distances less than approximately 430 km (the estimated *e*-folding scale). This conclusion about the dominant role of regional-scale processes is consistent with recent analyses of spatial patterns of covariation in survival rates of other salmon species (Myers et al. 1997; Coronado and Hilborn 1998; Peterman et al. 1998) and has important implications for future research. Efforts to identify relationships between environmental conditions and variation in survival rates should focus on processes and environmental variables that also show similar regional-scale patterns of covariation. Furthermore, inferences drawn by such investigations can be greatly enhanced by examining groups of stocks that show similar patterns of variation in survival rates, such as the groups identified in this paper (Myers 1998). Even without a knowledge of mechanisms or explanatory variables, it should be possible to obtain better estimates of stock–recruitment parameters by explicitly accounting for covariation among groups of stocks in multistock models (Walters 1986). Such an approach should improve estimates of appropriate escapement targets, reference points, forecasts of future recruitment, and estimates of the uncertainty in these measures.

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Developing Baltic cod recruitment models. I. Resolving spatial and temporal dynamics of spawning stock and recruitment for cod, herring, and sprat

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Abstract: The Baltic Sea comprises a heterogeneous oceanographic environment influencing the spatial and temporal potential for reproductive success of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the different spawning basins. Hence, to quantify stock and recruitment dynamics, it is necessary to resolve species-specific regional reproductive success in relation to size, structure, and distribution of the spawning stock. Furthermore, as species and fisheries interactions vary between areas, it is necessary to include these interactions on an area-specific basis. Therefore, area-disaggregated multispecies virtual population analyses (MSVPA) were performed for interacting species cod, herring (*Clupea harengus*), and sprat in the different subdivisions of the Central Baltic. The MSVPA runs revealed distinct spatial trends in population abundance, spawning biomass, recruitment, and predation-induced mortality. Results, when evaluated with respect to trends in population sizes from research surveys, were similar for the cod and sprat stocks but different for herring. Horizontal distributions from MSVPA runs and research surveys indicate that cod and sprat undergo migrations between basins during different life stages. This is an observation potentially influencing estimates for the different stock components but not affecting the overall stock sizes.

Résumé : La mer Baltique est un environnement océanique hétérogène qui influence la variation spatiale et temporelle du succès potentiel de la reproduction chez la Morue franche (*Gadus morhua*) et le Sprat (*Sprattus sprattus*) dans les différents bassins de fraye. Pour quantifier les stocks et la dynamique du recrutement, il est donc nécessaire de connaître la relation entre le succès de la reproduction régionale de chaque espèce et la taille, la structure et la répartition du stock des géniteurs. De plus, comme les interactions entre les espèces et la pêche varient d'une région à l'autre, il est nécessaire de les inclure région par région. Des analyses de populations virtuelles plurispécifiques (MSVPA), désagrégées quant à la région, ont été menées sur les espèces en interaction, la Morue, le Hareng (*Clupea harengus*) et le Sprat dans les différentes subdivisions de la Baltique centrale. Les MSVPA mettent en lumière des structures spatiales distinctes dans la densité de population, la biomasse des géniteurs, le recrutement et la mortalité due à la prédation. Lorsque les résultats sont évalués en tenant compte des tendances dans les tailles des populations obtenues par les inventaires scientifiques, ils sont semblables pour les stocks de Morue et de Sprat mais différents pour le Hareng. Les répartitions horizontales générées par les MSVPA et les inventaires scientifiques montrent que les Morues et les Sprats migrent d'un bassin à l'autre au cours de leur vie. Cette observation peut potentiellement affecter les estimations des différentes composantes des stocks mais non des densités totales des stocks.

[Traduit par la Rédaction]

Introduction

In the Baltic Sea, the spatial and temporal suitability of the spawning habitats of cod (*Gadus morhua*) vary dramatically with the oxygen conditions at the depth of incubation of the eggs (Nissling and Westin 1991; Wieland et al. 1994). As a consequence, the population dynamics of cod exhibit distinct trends in different areas of the Central Baltic (Sparholt and Tomkiewicz 2000), with a corresponding variation in predation pressure on its major prey species, herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Sparholt 1994). In turn, the population development of these plankti-

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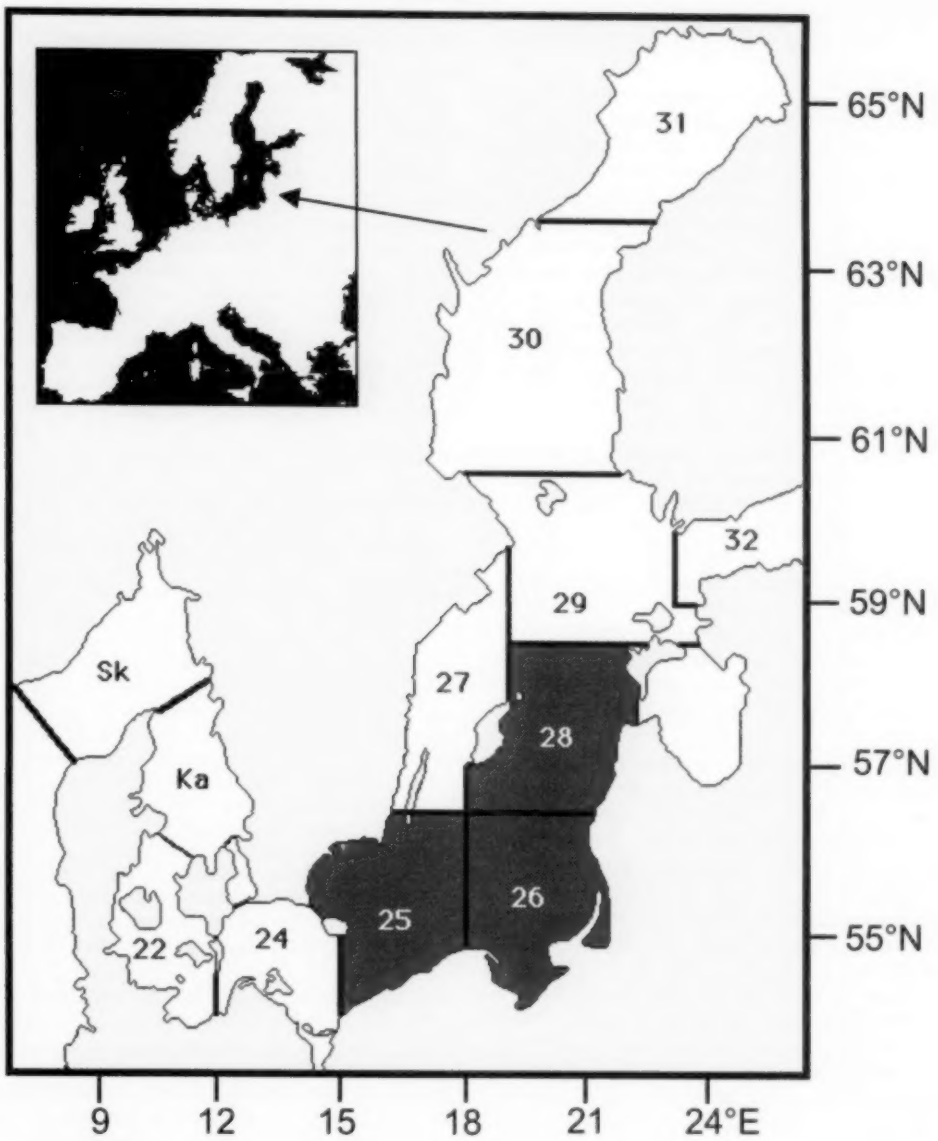
Fig. 1. Study area in the Baltic Sea with ICES subdivisions indicated.



vores determines the predation intensity on early life stages of cod (Köster and Möllmann 2000). Hence, to develop sustainable management strategies for the Central Baltic stocks, assessments and stock projections need to resolve and incorporate the effects of environmental variability and species interactions on reproductive success, in particular the potential for different spawning localities to contribute to recruitment success.

Multispecies virtual population analysis (MSVPA) has been applied addressing the biological interactions between fish stocks in the North Sea (Pope 1991; Stokes 1992) and the Baltic (Sparholt 1991, 1994). Sparre (1991) and Magnusson (1995) presented the theory and methods employed in the MSVPA as well as the underlying assumptions. The model considers predation by specific piscivores on their major fish prey species as biological interactions affecting the population dynamics of the prey stocks. In the Central Baltic, cod, herring, and sprat are the most important fish species and are presently the only species incorporated into the MSVPA (Sparholt 1994). Cod is assumed to be the top predator in the system, exhibiting cannibalistic behaviour, while herring and sprat are treated as prey species. These interactions are based on the analyses of the stomach contents of over 62 000 cod, the majority of samples originating from International Council for the Exploration of the Sea (ICES) Subdivisions 25, 26, and 28 in the Central Baltic (Fig. 1) collected during 1977–1993. At present, MSVPAs are run for two areas in the Baltic, a Western and a Central Baltic

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component to match the stock units used in the regular stock assessments (Neuenfeldt and Köster 2000), with the Central Baltic component dominating in terms of biomass and abundance (ICES 1998).

Within these two regions, the abundance and biological characteristics of the three species are heterogeneous both spatially (between subdivisions) and temporally (inter- and intra-annually). For example, population sizes of Central Baltic cod, as resolved by international bottom trawl (Sparholt and Tomkiewicz 2000) and ichthyoplankton surveys (Köster et al. 2001), have revealed distinct distributional trends. Furthermore, for cod, substantial differences in weight at age and maturity ogives have been reported for different subdivisions (ICES 1997*a*; Tomkiewicz et al. 1997). The abundance and characteristics of herring and sprat have also been observed to vary spatially and temporally in the different subdivisions of the Central Baltic (e.g., Ojaveer 1989). The herring stock in the Central Baltic is composed of a number of different spawning components exhibiting variations in spawning period and growth rates as well as meristic, morphometric, and otolith characteristics (e.g., Ojaveer 1981; Parmanne et al. 1994). For sprat, the existence of distinct populations is controversial, as deviations in growth rates observed between subareas have been explained by immigration from the western Baltic and by migration between different basins (Parmanne et al. 1994). However, other authors stated that sprat in the eastern Central Baltic form local populations (Ojaveer 1989), which can be separated, primarily by otolith characteristics (Aps et al. 1981).

In this study, we investigate the feasibility of conducting area-disaggregated MSVPA runs to resolve the dynamics of cod, herring, and sprat subpopulations in the different subdivisions (Fig. 1) corresponding roughly to the Central Baltic basins (Ojaveer and Elken 1995). The major objective of this exercise is to establish cod and sprat spawning population sizes in their different spawning regions, i.e., the Bornholm Basin located in Subdivision 25, the Gdansk Deep in Subdivision 26, and the Gotland Basin in Subdivision 28 (e.g., Ojaveer 1981; Bagge et al. 1994), as characterised by distinct hydrographic conditions (Bagge and Thurow 1993; MacKenzie et al. 2000). This exercise will thereby allow the investigation of regional reproductive success in relation to size and structure of the originating spawning population (Köster et al. 2001).

Resolution of a number of issues is necessary before determining the applicability of the area-disaggregated MSVPA approach. First is the validation of the area-disaggregated MSVPA results with respect to temporal trends in abundance and biomass of cod, herring, and sprat. In order to address this issue, results from trawl and hydroacoustic surveys are compared with the MSVPA output. Secondly, the impact of migration on population abundance may invalidate the approach. This issue is addressed by examining the relative horizontal distributions between subdivisions as determined by area-disaggregated MSVPA and research surveys. Finally, in order to assess the estimates relative to existing information of stock fluctuations, population sizes derived by the MSVPA runs were integrated over Subdivisions 25, 26, and 28 and compared with standard ICES stock assessments (ICES 1998).

Methods

Area-disaggregated MSVPA parameterisation

Cod, herring, and sprat in Subdivisions 25, 26, and 28 (Fig. 1) were assumed to be unit stocks composed of age-groups 0–9 for cod and herring and 0–7 for sprat with the oldest age-groups not handled as plus groups. Quarterly catch at age in numbers and weight at age in the catch were utilised for the different subdivisions for 1977–1992 as revised by ICES (1997*a*) with inputs for 1993–1996 based on national data reported to ICES (1997*b*). Weight at age in the catch was assumed to be equal to weight at age in the stock, exceptions being weight at age for cod age-groups 0 and 1. Here, due to size selection by commercial gear, mean values for the whole period were applied as determined by Sparholt (1991). To identify the spawning component of the stocks in the different basins, existing maturity estimates were employed. Maturity ogives for cod in different subdivisions represent averages over 5-year periods available from 1980 onwards for combined sexes (Tomkiewicz et al. 1997). As no data are at present available for the period 1977–1979, estimates from the period 1980–1984 were applied. For herring and sprat stocks, maturity ogives were assumed to be constant over time and the estimates used are those previously employed for these stocks in the Baltic (ICES 1997*b*).

Estimates of cod predation on herring and sprat as well as of cannibalism are based on quarterly cod stomach content data by subdivision as revised in ICES (1997*a*). Average age-specific quarterly consumption rates were estimated by subdivision as described in ICES (1999*a*). The residual natural mortality rate was assumed to be 0.2·year^{-1}, equally distributed over quarters, corresponding to standard MSVPA runs in the Baltic (Sparholt 1991). Suitability coefficients of prey species age-groups as food of specific predator age-groups (Sparre 1991) were estimated according to the standard suitability submodel implemented in the Baltic MSVPA (ICES 1997*a*). The tuning of the MSVPAs was performed by iteratively running extended survivor analyses (Shepherd 1999) and MSVPAs exchanging updated terminal fishing and predation mortalities until convergence was achieved (Neuenfeldt and Köster 2000). Abundance indices utilised for tuning originated from the international bottom trawl survey directed to cod, performed annually in February–March (Sparholt and Tomkiewicz 2000), and the international hydroacoustic survey directed to herring and sprat, conducted annually in September–October (ICES 1998).

Validation of area-disaggregated MSVPA results

To assess the feasibility of employing the area-disaggregated MSVPA for resolving temporal trends of stock abundance in the different basins, results from the model are compared with trawl and hydroacoustic surveys estimates. Data from these sources fall into two categories: those being data used to tune the area-disaggregated MSVPA, thus nonindependent, and data not employed for tuning purposes. The international surveys utilised for tuning, although having an impact on the MSVPA results during the later part of the time series, have a reduced effect on the outputs back in time. This feature makes these data valid for a comparison of trends for a major part of the time series.

As a second mode of validation, independent population size indices are available from other research surveys, e.g., directed to spawning concentrations and young fish abundance. These indices, although independent, are typically not focused on monitoring population sizes and hence are of a lower quality than the nonindependent data designed for this task. For the purposes of validation, however, these sources are applicable for examining trends in abundance.

The third method of validation involves the temporal coherence of population abundance and structure in the various basins. The comparison of relative horizontal distributions and corresponding age structures of the different subpopulations from area-

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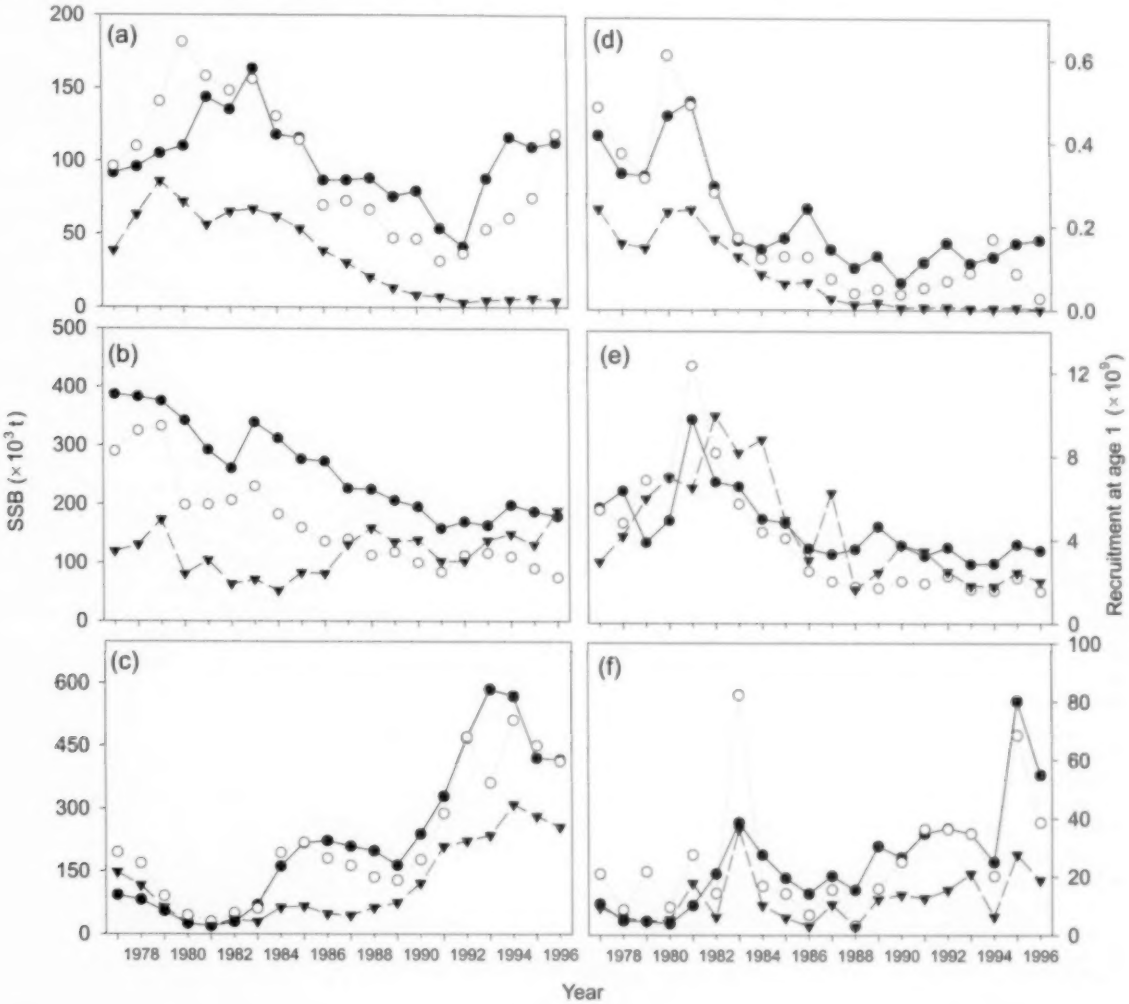
Fig. 2. SSB (second quarter) of (*a*) cod, (*b*) herring, and (*c*) sprat and recruitment at age 1 (beginning of the year) of (*d*) cod, (*e*) herring, and (*f*) sprat from area-disaggregated MSVPA in different subdivisions of the Central Baltic Sea (solid circles, Subdivision 25; open circles, Subdivision 26; triangles, Subdivision 28).



disaggregated MSVPA runs and corresponding research surveys will validate the suitability of the approach regarding age-specific migration between subdivisions.

Finally, spawning stock sizes and recruitment derived by the area-disaggregated MSVPAs were summed over Subdivisions 25, 26, and 28 and compared with corresponding estimates from the standard stock assessment for the Central Baltic. These are comparable, as the standard assessment utilises predation mortalities from area-aggregated MSVPAs as input. This exercise resolves whether the approach of running a suite of independent MSVPAs generates robust results when compared with the best available information on stock development.

Results

Output from area-disaggregated MSVPA runs

Spawning populations

Spawning stock biomass (SSB) values for cod, herring, and sprat in the different subdivisions from the area-disaggregated MSVPA runs are presented in Fig. 2 and Appendix Table A1. The Central Baltic cod stock displayed a substantial decrease in SSB in all three areas from 1983 onwards. The SSB increased again in the early 1990s in Subdivisions 25 and 26 due to enhanced reproductive success and a reduction in fishing mortality; however, no recovery was evident in Subdivision 28.

The herring SSB in Subdivisions 25 and 26 showed a more or less continuous decline to less than half of the original level from the beginning of the time series until the early 1990s. Thereafter, the SSB stabilised, being substantially lower in Subdivision 26. The SSB in Subdivision 28 exhibited an increase in stock size in the second half of the time series, reaching spawning stock sizes similar to those in Subdivision 25 in most recent years.

The SSB of sprat in Subdivisions 25 and 26 showed a rather similar time trend, with an increase from very low

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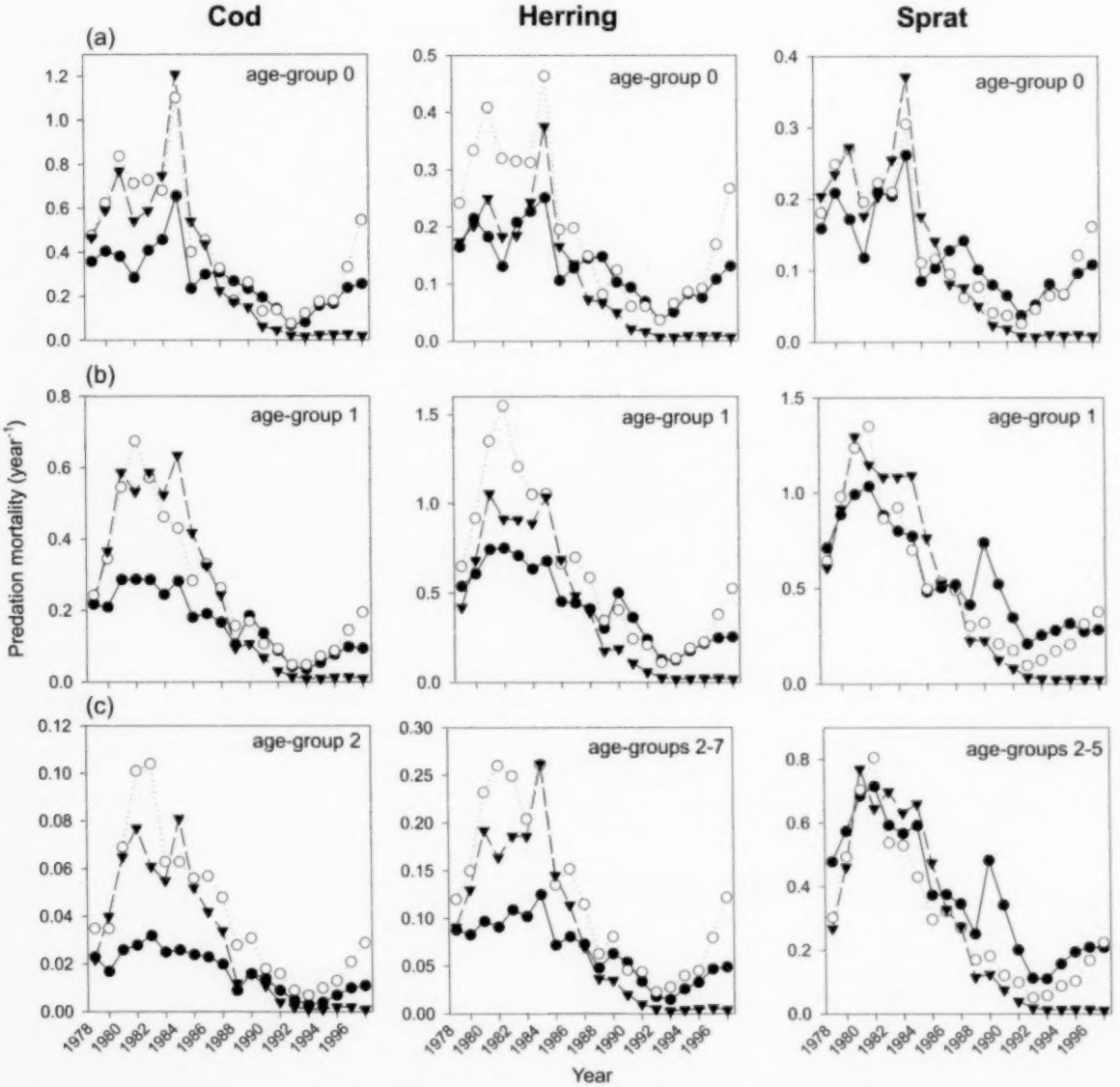
Fig. 3. Annual predation mortality rates of cod, herring, and sprat (*a*) age-group 0, (*b*) age-group 1, and (*c*) cod age-group 2, herring age-group 2–7, and sprat age-group 2–5 from area-disaggregated MSVPA in different subdivisions of the Central Baltic Sea (solid circles, Subdivision 25; open circles, Subdivision 26; triangles, Subdivision 28). Note that predation mortality of the 0-group refers to the third and fourth quarters.



levels in the beginning of the 1980s to stable intermediate values in the second half of the decade. In the beginning of the 1990s, a substantial increase in the spawning stock is estimated for both areas. In Subdivision 28, fluctuations in the SSB were much less pronounced; however, the general trend was rather similar to that in Subdivisions 25 and 26.

Recruitment

Estimated recruitment of cod, herring, and sprat at age 1 for the different subdivisions is displayed in Fig. 2 and Appendix Table A1. A declining trend in cod recruitment is evident in the 1980s for all areas. The abundance of 1-group cod was estimated to be lowest in Subdivision 28 throughout the time series, with extremely low estimates of recruitment in this subdivision since 1990. During the second half of the time series, cod recruitment was estimated to be highest in Subdivision 25 (with the exception of the 1993 year-class). An increase in recruitment from 1990 to 1994 is visible for Subdivision 26, followed by a decline in recent years.

Trends of herring recruitment to age 1 are in general similar in all subareas, with a decline throughout the decade from maximum values during the beginning of the 1980s. Thereafter, recruitment stabilised in all areas, being highest in Subdivision 25 and lowest in Subdivision 26.

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Sprat recruitment was variable during the early part of the time series, with an outstanding year-class evidenced in 1982. During this period, recruitment in Subdivision 26 was in general highest. Since 1982, recruitment in Subdivision 28 was estimated to be the lowest, with a less pronounced increase in reproductive success than in the other basins after the late 1980s. Recruitment success in Subdivisions 25 and 26 has shown a similar trend since 1990, first with intermediate and finally with high recruitment.

Predation mortality

A substantial difference in cod cannibalism rates between areas is apparent (Fig. 3), with the lowest predation on cod estimated for 1978–1985 in Subdivision 25. Furthermore, age-specific differences in predation mortality are pronounced, with cannibalism rates on 0-group cod being considerably higher than on 1-group cod. Predation on 2-group cod was in general low, i.e., less than 50% of the applied residual mortality of 0.2. In Subdivision 28, cannibalism rates declined from maximum values in 1983 to extremely low values in the 1990s.

Predation rates of cod on herring (Fig. 3) were highest in Subdivision 26 in the beginning and at the end of the time series, independent of prey age. In all areas, predation mortality rates declined throughout the 1980s to lowest levels in early 1990s, with a subsequent increase in most recent years in Subdivision 25 and 26, while predation in Subdivision 28 remained rather low. Estimated predation mortality rates were in general highest for 1-group herring, intermediate for 0-group herring, and comparatively low for older herring.

Maximum predation pressure on 0-group sprat occurred in 1983 and on older age-groups 3–4 years earlier (Fig. 3). Independent of the prey age, a decrease in predation mortality occurred until 1991, with a subsequent increase in recent years in Subdivisions 25 and 26. Cod predation on juvenile sprat was of a similar magnitude to that estimated for herring, while predation mortality rates of adult sprat were considerably higher than for adult herring.

Validation of area-disaggregated MSVPA results

Validation employing trawl and hydroacoustic surveys used for MSVPA tuning

Significant linear relationships were obtained between area-disaggregated MSVPA estimates of cod population size (age-group 2+) (Appendix Table A1) and abundance indices based on bottom trawl surveys (Appendix Table A2) in all three subareas (Fig. 4), with the lowest r^2 values observed in Subdivision 25 ($r^2 = 0.64$), intermediate in Subdivision 26 ($r^2 = 0.69$), and highest in Subdivision 28 ($r^2 = 0.80$). Intercepts were significant for Subdivisions 26 and 28 ($p = 0.039$ and 0.041) but not in Subdivision 25 ($p = 0.052$). Large interannual variability was observed in the international trawl survey in Subdivision 25 in 1980–1982 and 1985–1987, causing large deviations between observed and modelled population abundance. Similarly, in Subdivision 26, considerable deviations occurred in the beginning of the time series, with a high trawl survey abundance index in 1982 and a relatively low one in 1983. Interestingly, in Subdivision 28, the 1983 survey revealed the highest abundance indices on record, potentially indicating a shift in distribution compared with 1982 and subsequent years. Apart from this observation, evidence of interannual shifts in distribution between different subareas is not apparent. Correlating the age-specific abundance values obtained from the area-disaggregated MSVPA runs against corresponding indices from the trawl survey revealed a dome-shaped pattern of r^2 values with age, being lowest in the oldest age-groups. This might indicate tuning problems encountered for these age-groups, while the decreasing fit in younger age-groups can be explained mainly by trawl selectivity. Cod recruitment estimates at age 1 derived by area-disaggregated MSVPA runs (Appendix Table A1) were nevertheless significantly correlated with abundance indices from the survey (Appendix Table A3), with highest variability in Subdivision 25 (Table 1). Here, an especially low abundance index of the 1979 year-class in the 1980 survey does not coincide with high recruitment estimated by the area-disaggregated MSVPA. Excluding this year-class from the correlation improved the relationship between both recruitment estimates considerably ($r^2 = 0.60$).

In contrast with cod, correlation between abundance estimates of herring from area-disaggregated MSVPA runs (Appendix Table A1) and hydroacoustic surveys (Appendix Table A2) revealed no significant relationships for any of the subdivisions (Fig. 4).

For sprat, the comparison between international hydroacoustic survey results (Appendix Table A2) and area-disaggregated MSVPA output (Appendix Table A1) revealed trends similar to those observed for cod (Fig. 4), also with lowest r^2 values in Subdivision 25 ($r^2 = 0.59$) and highest in Subdivision 28 ($r^2 = 0.80$). The increase in population size in the 1990s observed in the MSVPA estimates for Subdivision 25 is less pronounced in the hydroacoustic surveys. In particular, the survey estimate obtained in 1992 appears to be rather low. Due to technical and area coverage problems, the hydroacoustic surveys in 1992 and 1993 (the latter omitted here) have been suggested to be the most unreliable in the present time series and are in fact excluded from regular assessment runs (ICES 1997*b*). In Subdivision 28, contrary to Subdivision 25, the increase in population size in recent years is more pronounced in the hydroacoustic survey than in the area-disaggregated MSVPA. A similar comparison for sprat recruitment at age 1 (Appendix Tables A1 and A3) revealed significant correlations for all subareas, with highest r^2 values in Subdivision 25 and lowest in Subdivision 28 (Table 1). In the latter area as well as in Subdivision 26, large deviations occurred for the 1982 year-class, with the MSVPA estimates being significantly higher. Excluding this year from the correlation increased the r^2 values considerably (0.65 in Subdivision 26 and 0.79 in Subdivision 28). Thus, recruitment of the 1982 year-class appears to be severely overestimated by the area-disaggregated MSVPA, while in general, hydroacoustic- and MSVPA-derived recruitment estimates are in good agreement.

Validation employing independent research surveys

Validation of the area-disaggregated MSVPA estimates for cod was performed against Latvian bottom trawl surveys conducted in Subdivisions 26 and 28 in January and November–December during 1976–1991 (Appendix Table A2). These estimates of age-group 3+ cod abundance were significantly correlated with the corresponding area-disaggregated MSVPA

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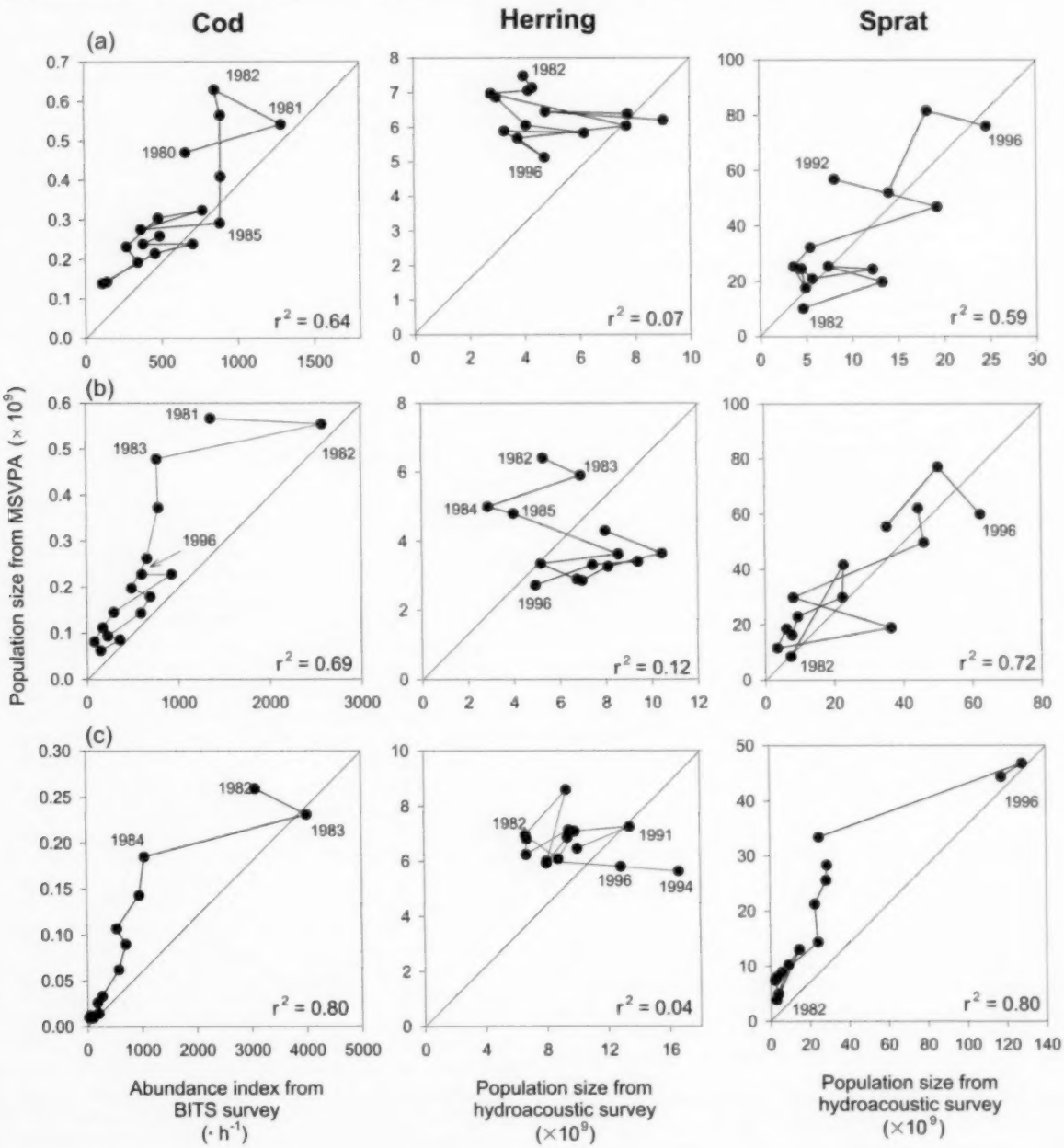
Fig. 4. Population sizes of cod (age-group 2+), herring (age-group 1+), and sprat (age-group 1+) derived by area-disaggregated MSVPA at the time of survey versus abundance indices from tuning fleets. (*a*) Subdivision 25; (*b*) Subdivision 26; (*c*) Subdivision 28. The coefficient of determination (r^2) is from a linear regression model, allowing for an intercept. BITS, Baltic international trawl survey.



output (Fig. 5), with r^2 values ranging from 0.52 to 0.90. Despite these significant relationships, a number of noteworthy deviations were evident. Outstandingly high abundances of 3+ cod in Subdivision 28 were encountered in the trawl surveys in January 1983, a result not reflected in the MSVPA estimates. In Subdivision 26, a reverse situation was encountered, with comparatively low catch rates in January and November–December 1983 as compared with high population abundance estimated by the MSVPA. These results may indicate an anomalous distribution of the stock in 1983 as in the previous section identified by the international bottom trawl survey.

Further corroborative results come from Latvian demersal trawl surveys on cod spawning concentrations in the Gotland Basin (Uzars et al. 1991). These show a decline in biomass indices of 84% during the period 1980–1989, a result corre-

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Table 1. Linear regressions performed to validate cod and sprat recruitment (age-group 1) from area-disaggregated MSVPA (dependent variable) (numbers) using results from the international bottom trawl survey for cod (no.·h^{-1}) and the international hydroacoustic survey for sprat (numbers), parameter estimates, and their significance level and r^2 value.

Subdivision	Year-classes	Parameter	Parameter estimate	p	r^2
Cod					
25	1979–1995	Slope	6.2329×10^6	0.015	0.34
		Intercept	1.4396×10^8	<0.001	
26	1980–1995	Slope	3.2003×10^6	<0.001	0.73
		Intercept	9.1831×10^7	<0.001	
28	1981–1995	Slope	8.3191×10^6	<0.001	0.88
		Intercept	98 953	<0.001	
Sprat					
25	1981–1995	Slope	5.4102	<0.001	0.68
		Intercept	2.1162×10^{10}	<0.001	
26	1981–1995	Slope	1.3676	0.012	0.42
		Intercept	1.1497×10^{10}	0.146	
28	1981–1995	Slope	0.2798	0.002	0.35
		Intercept	9.8700×10^{10}	0.024	

Fig. 5. Population sizes of cod (age-group 3+) derived by area-disaggregated MSVPA versus abundance indices from the Latvian bottom trawl survey in Subdivisions (SD) 26 and 28. (*a*) January; (*b*) November–December. The coefficient of determination (r^2) is from a linear regression model, allowing for an intercept.

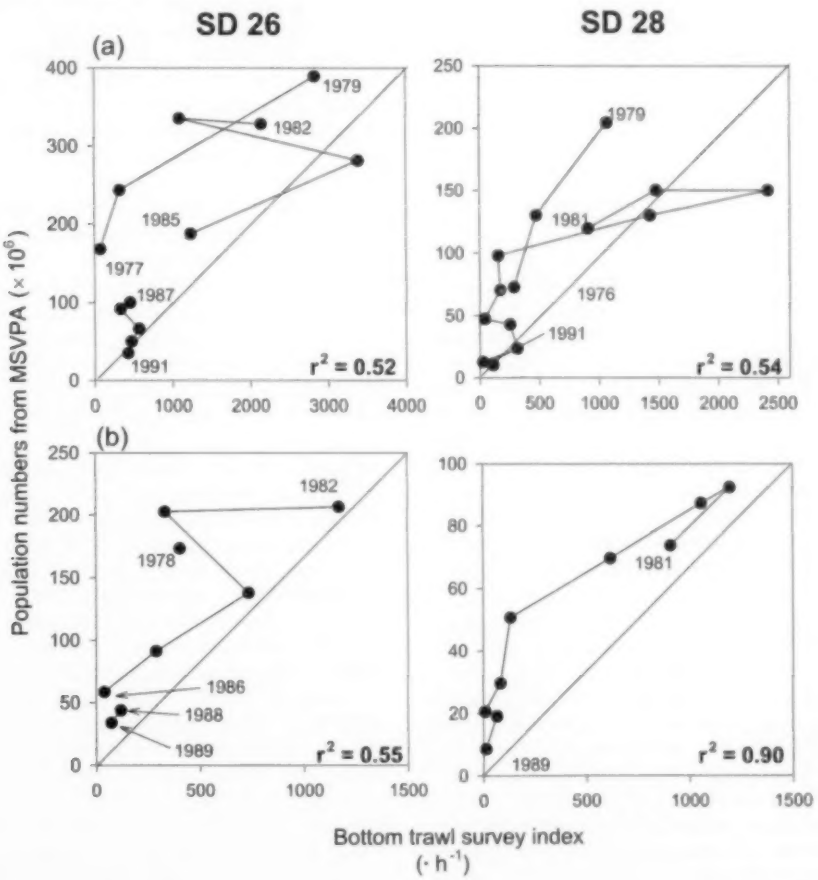

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Table 2. Comparison of sprat biomass estimates (age-group 1+) (kt) in different subdivisions (SD) as derived from hydroacoustic surveys in May–June and area-disaggregated MSVPA (second quarter).

	SD 25		SD 26		SD 28	
Year	Survey	MSVPA	Survey	MSVPA	Survey	MSVPA
1979	161	56	118	104	162	49
1981	68	73	76	101	41	51
1982	149	143	70	83	110	40
1984	159	341	120	319	147	92
1985			152	285	173	84
1986	153	295	128	215	165	63
1995	465	722	560	737	440	448

Note: An empty cell indicates that a reliable survey was not conducted during that period.

sponding to a similar decline of the SSB derived by the area-disaggregated MSVPA for the same period. Catch rates from pelagic trawl surveys covering the Bornholm Basin at different times of the spawning season revealed on average a 53% reduction in abundance of sexually mature cod from 1995 to 1996 (ICES 1999*b*), a trend that is not obvious from the area-disaggregated MSVPA. Comparing the daily egg production at peak spawning time as derived by ichthyoplankton surveys with corresponding potential annual egg production from 1986 to 1996 (Köster et al. 2001) revealed maximum egg production by both methods in the Bornholm Basin in 1994 and 1995. In 1996, a large potential egg production (only 5% lower than the maximum in 1994) is contrasted by a 46% lower egg production as obtained from the ichthyoplankton survey. This indicates an overestimation of the most recent cod population size obtained by the area-disaggregated MSVPA for Subdivision 25.

Unfortunately, hydroacoustic surveys by the former GDR/USSR conducted in May–June 1979–1986 (Sjöstrand 1989) are not representative of the abundance of herring. The majority of the spring-spawning herring aggregate outside the survey area on their spawning grounds during this period (e.g., Aro 1989; Parmanne et al. 1994), making these observations unreliable for estimating abundance and distribution. Other independent survey information, e.g., the Polish young fish survey, either showed high interannual variability (ICES 1998) or did not cover comparable areas or sufficient time periods (Sjöstrand 1989). Thus, the available independent data on herring abundance appear to be insufficient for validation of the area-disaggregated MSVPA results.

Validation of area-disaggregated MSVPA derived biomass values of sprat were performed using above-mentioned hydroacoustic surveys (Table 2) conducted in May–June 1979–1986 (data compiled by Sjöstrand 1989) as well as Danish and Russian hydroacoustic surveys conducted in May–June 1995 (J. Tomkiewicz, Institute of Marine Sciences, Kiel, Germany, personal communication; T.G. Vasilieva, Atlantic Scientific Research Institute of Marine Fisheries and Oceanography, Kaliningrad, Russia, personal communication). The correlation between area-disaggregated MSVPA output and hydroacoustic survey results was high in all subdivisions (r^2 = 0.83 to 0.91), driven mainly by the increase in stock biomass from the mid-1980s to 1995.

Population spatial dynamics

In order to validate the spatial distribution of adult cod in the Central Baltic, the area-specific relative abundance of age-group 3+ from bottom trawl surveys in February–March (Sparholt and Tomkiewicz 2000) is plotted against the relative population abundance from the area-disaggregated MSVPAs (Fig. 6). In Subdivision 26, the population remained stable throughout the time period, with the highest abundance observed in both the trawl survey and MSVPA estimates in 1996. In Subdivision 25, the proportions estimated by the MSVPA were in general higher than that observed in the trawl surveys, whereas in Subdivision 28, the MSVPA estimates were in general lower. Within the latter area, a clear time trend of decreasing importance of the stock component is indicated by both data sources, with recent years being similarly low in the area-disaggregated MSVPA and trawl survey results.

Cod recruits (age-group 1) showed a different distribution pattern than did adult cod. Highest proportions were encountered by the trawl survey in Subdivision 26, while the MSVPA estimated intermediate proportions (Fig. 6). On the contrary, in Subdivision 25, the MSVPA-derived recruitment is in general high and the corresponding fractions in the trawl surveys are comparatively low, with a time trend of increasing importance of the area determined by the former but not by the latter. For Subdivision 28, independent of the method, rather similar low proportions were calculated, especially in recent years. The distribution pattern of age-group 2 by the area-disaggregated MSVPA changed only slightly from that of age-group 1. However, in the trawl survey, considerable changes with age were observed, with increased proportions in Subdivisions 25 and 28 and decreased proportions in Subdivision 26.

The higher fraction of the cod stock derived by the trawl surveys in Subdivision 28 and a lower fraction in Subdivision 25 may be interpreted as a spawning migration from the Gotland Basin to the Bornholm Basin taking place after the bottom trawl survey is performed in the first quarter. These migrations have been previously described (Lablaika and Lishev 1961).

The distribution pattern from the trawl survey changes with age, i.e., recruits of age-group 1 concentrate in Subdivision 26. A biological explanation for this dislocation relative to the area-disaggregated MSVPA results may be a drift of larvae and pelagic juveniles out of the Bornholm Basin into the neighbouring subdivision, which has been identified through the application of hydrodynamic models (Voss et al. 1999; Hinrichsen et al. 2001). The change in relative distribution of age-group 2 indicates either a higher mortality of juveniles in Subdivision 26, not accounted for in the MSVPA, or a movement out of the area. In fact, an analysis of catch rates obtained from Latvian trawl surveys conducted at different times of the year in the Gotland Basin (see above) revealed indications of an expansion of juvenile cod into the Gotland Basin from southern areas.

The relative distribution of herring obtained by hydroacoustic surveys in September–October and that of the area-

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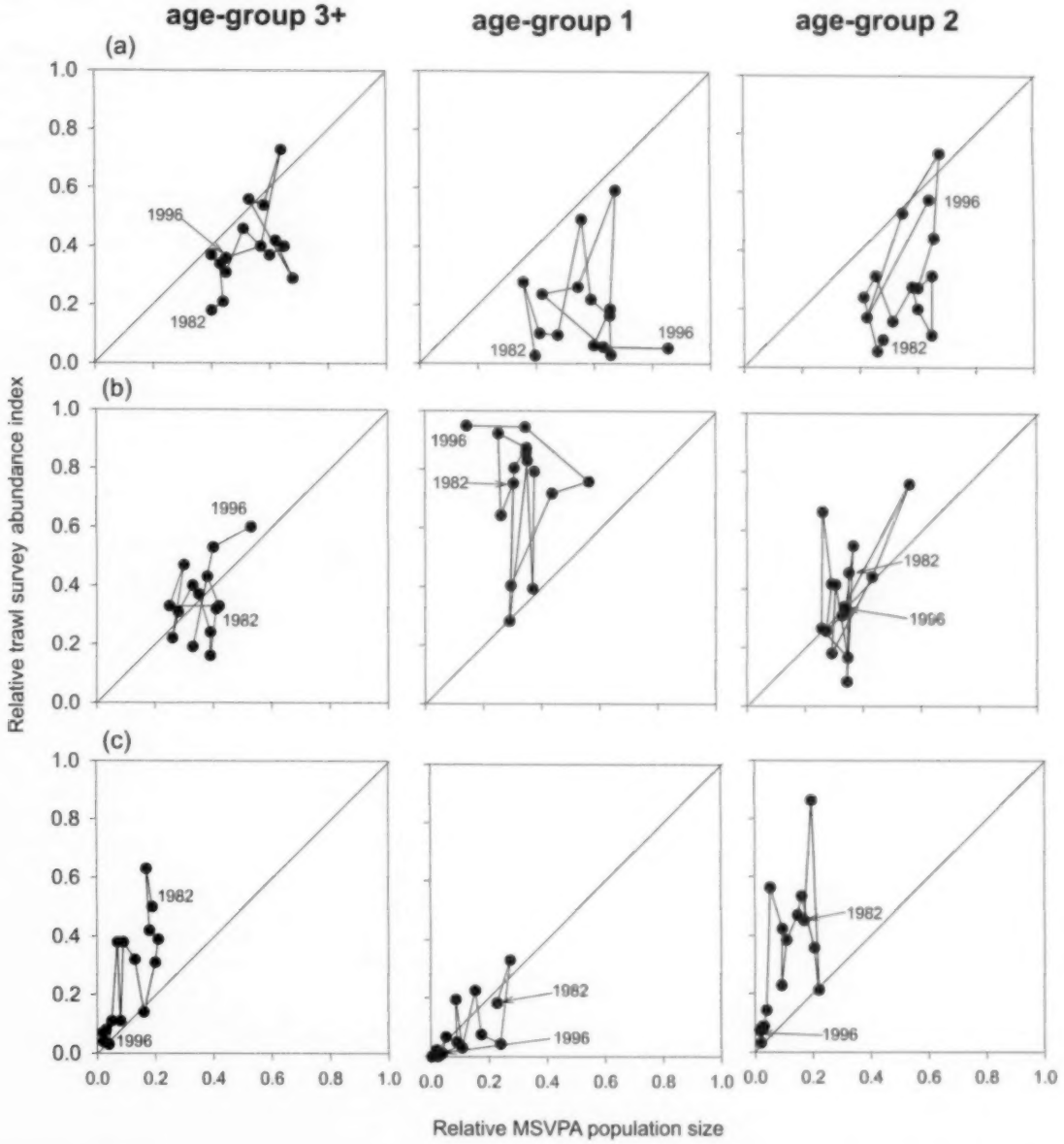
Fig. 6. Relative horizontal distributions of total cod abundance indices (age-groups 3+, 1, and 2) from the Baltic international trawl survey versus corresponding relative distributions estimated by area-disaggregated MSVPA. (*a*) Subdivision 25; (*b*) Subdivision 26; (*c*) Subdivision 28.



disaggregated MSVPA match on average for Subdivision 28, whereas the fraction inhabiting Subdivision 25 estimated by the MSVPA was slightly higher (Fig. 7). Pronounced long-term changes in the relative distribution of the herring populations were not obvious in any of the time series. Although not commonly agreed, it has been argued (e.g., Ojaveer 1989) that there exist three distinct herring groups in the Baltic, the open sea and the coastal spring-spawning herring as well as the autumn-spawning herring, represented by various independent stocks, showing different migration patterns. Additionally, the intensity of these migrations depends on environmental conditions and food supply (Parmanne et al. 1994). Hence, due to this complex stock structure and the migratory behaviour of herring within and between subdivisions (e.g., Aro 1989; Ojaveer 1989), an evaluation of the obtained relative distribution patterns from the area-disaggregated MSVPA is extremely difficult.

When repeating the exercise for sprat using the international hydroacoustic survey of September–October, a picture similar to that for cod is obtained. Higher proportions are es-

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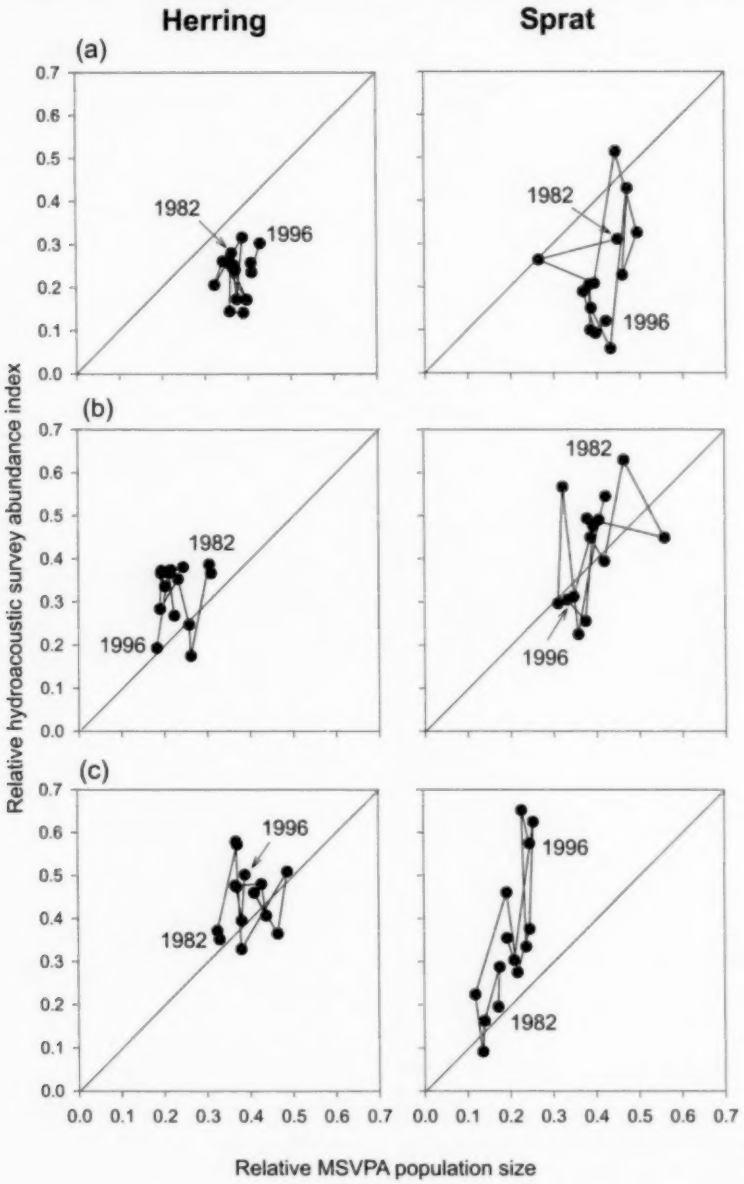
Fig. 7. Relative horizontal distributions of total herring and sprat abundance (age-group 1+) from the international hydroacoustic survey versus corresponding relative distributions derived by area-disaggregated MSVPA. (*a*) Subdivision 25; (*b*) Subdivision 26; (*c*) Subdivision 28.



timated for Subdivision 25 by the MSVPA and lower abundance in Subdivision 28, with increasing deviations with time, and on average similar fractions in Subdivision 26 (Fig. 7). A comparison of the average distribution patterns obtained from both data series with corresponding values derived by hydroacoustic surveys in May–June 1979–1986 (ICES 1999*a*) shows that the similarity to the area-disaggregated MSVPA output is considerably greater than to the hydroacoustic survey in autumn. The former allocated on average 37% of the stock to Subdivision 25 and 42% to Subdivision 26. The survey in May–June revealed a corresponding fraction of the stock inhabiting Subdivision 25 and on average similar population levels in both eastern areas. In contrast, the hydroacoustic survey in September–October identified the highest population sizes to be in Subdivision 26 (52%) and considerably lower fractions of the stock in Subdivision 25 (26%). This could be interpreted as spawning migrations from Subdivision 26 into the Bornholm Basin and the central Gotland Basin. However, when interpreting the encountered deviations in relative distributions, an exchange between noncovered Subdivisions 27 and 29 and the study area must be considered. Additionally, sprat from the

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western Baltic migrate to some extent to the Bornholm Basin for spawning (Aro 1989; Parmanne et al. 1994).

Comparison of standard stock assessment and area-disaggregated MSVPA results

Standard assessment results for the Central Baltic cod stock (Subdivisions 25–32), the Central Baltic herring stock (Subdivisions 25–29 and 32, including the Gulf of Riga), and the Baltic sprat stock (Subdivisions 22–32) (ICES 1998) allow validation of the output of the area-disaggregated MSVPA (summed over Subdivisions 25, 26, and 28). The standard assessment utilises area-aggregated MSVPA derived predation mortalities as input and is thus comparable with the integrated results obtained by the area-disaggregated MSVPAs. However, stock units for all three species are not the same, as the regular assessment also includes at least Subdivisions 27, 29, and 32. The major part of the cod catch (90–98%) is nevertheless taken in the areas covered by the present study (Sparholt and Tomkiewicz 2000).

Herring population estimates for Subdivisions 25–28 can be obtained from standard assessment results (ICES 1998) encompassing Subdivisions 25–29 and 32, when subtracting stock estimates for Subdivisions 29 and 32 determined by ICES (1998). However, Subdivision 27 is still included as an area that sustains a substantial herring fishery and for which the international hydroacoustic survey on average estimates 21% of the entire population in the Central Baltic.

The standard assessment of sprat treats the entire Baltic as one stock unit. To account for sprat in the western Baltic (Subdivisions 22–24), population estimates derived by an earlier MSVPA (ICES 1997*a*) were subtracted from the estimates for the entire Baltic. Subdivisions 25, 26, and 28 covered in the present study sustain the major part of the sprat catch in the Baltic (79–83% in recent years). Nevertheless, the area-disaggregated MSVPA population sizes should to a certain degree underestimate the Central Baltic sprat stock compared with the standard assessment (excluding Subdivisions 22–24), as Subdivisions 27, 29, and 32 are still not included.

Standard assessment and area-disaggregated MSVPA derived estimates of cod SSB show a similar development from 1986 to 1995 (Fig. 8). The standard assessment estimates are in general slightly higher, due to the incomplete area coverage by our disaggregated multispecies assessment. A relatively large discrepancy occurred in 1996, with the regular assessment estimate being substantially lower. This result confirms the overestimation by the area-disaggregated MSVPA of the population size in Subdivision 25 in recent years (described above). In the first part of the time series, considerably higher SSB values were estimated by the standard assessment. This cannot be explained by the lack of inclusion of Subdivisions 27, 29, and 32 in the present area-disaggregated MSVPA runs. Other factors, e.g., differences in the recompiled catch and especially weight at age data (see below), obviously contribute to this deviation.

For herring, the trends in SSB estimates from standard assessment and area-disaggregated MSVPA were rather similar, with a less rapid decline in the stock predicted by the latter (Fig. 8). The difference between the estimates from Subdivisions 25–28 and the area-disaggregated MSVPA output are higher than expected from the lack of area coverage, which is caused by deviations in the revised and the standard assessment catch at age database (ICES 1999*a*).

Standard assessment and area-disaggregated MSVPA estimates for sprat SSB are relatively similar throughout the entire time series (Fig. 8). Until 1983, the standard assessment SSBs are higher than the corresponding multispecies estimates; this could be expected due to the differences in area coverage. However, since 1984 the area-disaggregated MSVPA derived spawning stocks are in general slightly higher.

Cod recruitment estimates derived by both assessments (age-group 2) were similar throughout the time series (Fig. 9). This clearly demonstrates that the large deviations encountered in the SSB early in the time series are generated to a large extend by deviations in weight at age in the stock. These are set as constant in the regular assessment before 1983.

For herring, standard assessments give an impression with respect to recruitment (age-group 1) development similar to our multispecies assessment until the mid-1980s but show increasing differences afterwards (Fig. 9). As expected, recruitment values generated by the area-disaggregated MSVPA runs were in general lower. However, especially in the beginning of the time series, the deviation was less than expected. This indicates that the major changes in SSB during this period were to a large extent due to deviations in weight at age.

Sprat recruitment (age-group 1) as determined by both methods was rather similar in all years considered. The area-disaggregated MSVPA revealed in general slightly higher values, with the exception of recent years (Fig. 9).

Discussion

The results of the area-disaggregated MSVPA runs performed here revealed distinct trends in population abundance, spawning biomass, recruitment, and predation mortalities of cod and sprat in different areas of the Central Baltic. These results were in general similar to time trends in population sizes of cod and sprat as estimated by standard assessments, research surveys utilised for tuning of the MSVPA runs, as well as independent estimates of stock abundance. The application of the area-disaggregated MSVPA was inconclusive for Baltic herring stocks due to timing and area coverage of surveys, complexity of stock structure, and migratory behaviour. Hence, due to the limited amount of other suitable data series on herring abundance, a conclusive validation of distribution of the stock appears at present to be impossible. The area-disaggregated MSVPA does, however, capture the temporal dynamics of the Baltic herring population as estimated by the standard assessment.

A number of data-related and methodological problems impact upon the utility of the present approach for cod and sprat. For example, the newly compiled catch at age data for cod and sprat (ICES 1997*a*) showed considerable fluctuations in some age-groups, quarters, and years. High variability in the catch in numbers of the last age-group of cod caused problems in tuning the terminal fishing mortality values. For sprat, tuning of the last year in the time series was problematic in Subdivisions 25 and 26 due to trends in fishing mortality at age as well as changes in the exploitation

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Fig. 8. SSB derived by area-disaggregated MSVPA and standard stock assessments (XSA) (both at the beginning of the year) of (*a*) cod, (*b*) herring, and (*c*) sprat (solid circles, MSVPA; open circles, XSA for standard assessment areas; triangles (Fig. 8*b*), XSA Subdivisions 25–28). See text for a detailed description of standard assessment areas.

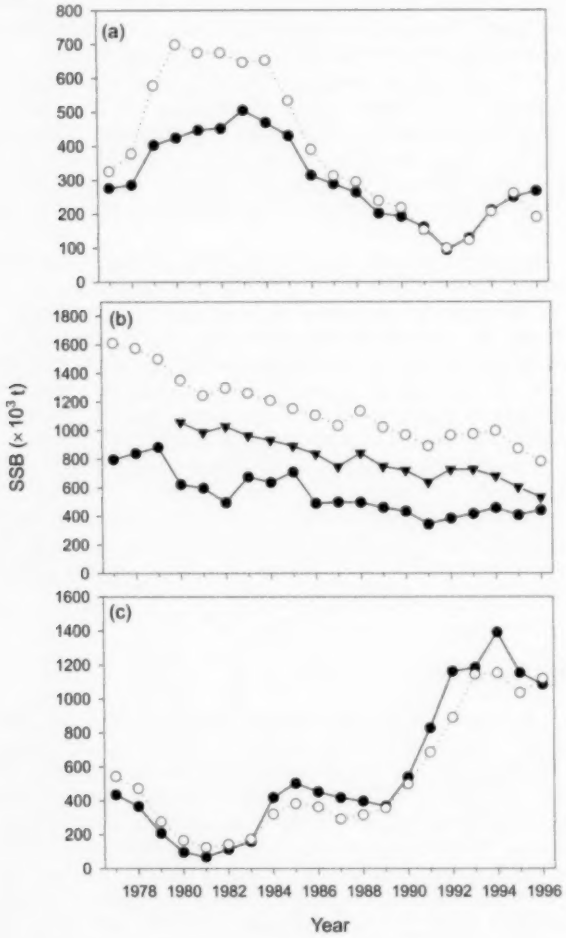
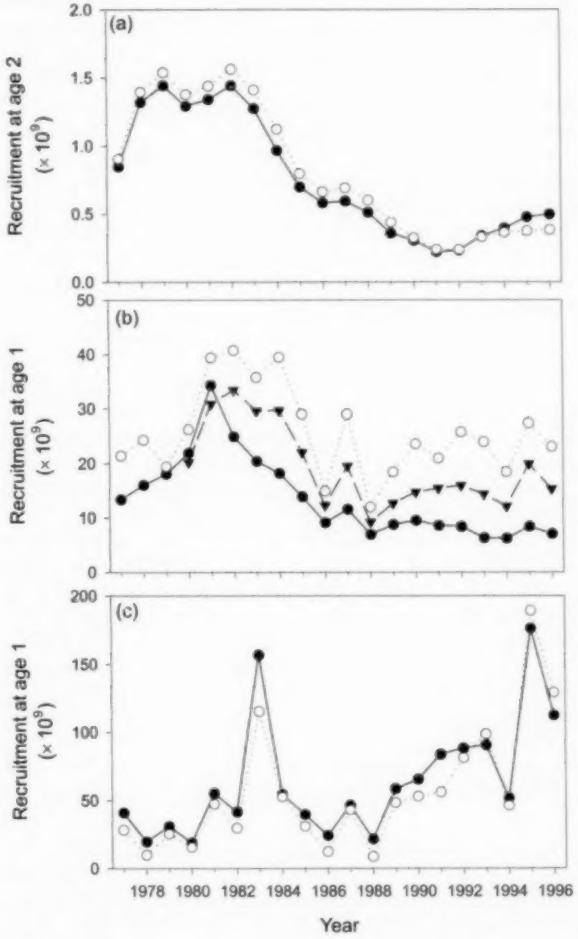


Fig. 9. Recruitment derived by area-disaggregated MSVPA and standard stock assessments (XSA) (beginning of the year) of (*a*) cod, (*b*) herring, and (*c*) sprat (solid circles, MSVPA; open circles, XSA for standard assessment areas; triangles (Fig. 9*b*), XSA Subdivisions 25–28). See text for a detailed description of standard assessment areas.


(a)
(b)
(c)
Recruitment at age 2 (× 10⁹)
Recruitment at age 1 (× 10⁹)
Recruitment at age 1 (× 10⁹)
Year
1978 1980 1982 1984 1986 1988 1990 1992 1994 1996

pattern (ICES 1998) caused by the commencement of a large-scale reduction fishery.

The virtual population analysis technique assumes that catch at age data are exact input data, which due to several reasons is seldom the case. The present analysis covers a time period with well-established reporting systems in the Baltic introduced in the mid-1970s. The data compilation procedure utilising information submitted by the responsible national laboratories is described in detail in ICES (1997*a*, 1999*a*). However, discarding and misreporting take place in Baltic cod and are not accounted for in the present catch at age data. The estimated discards of age-group 1–2 in 1998 and 1999 amounted to 17 and 4%, 9 and 2%, and 3 and 2% of the total catch in numbers in Subdivisions 25, 26, and 28, respectively (ICES 2000). These preliminary data indicate considerable interannual variability in discards and a potential bias of recruitment estimates in years of intensive discarding. Misreporting in the cod fishery has been identified by ICES (1997*b*) especially for the period 1992–1994 with restrictive fisheries management measures enforced. Misreporting is partly accounted for by national catch estimates treated in the assessment as unallocated catches according to subdivision. However, for the above period, a considerable underestimation of the catch may have nevertheless occurred, affecting the spawning stock size estimation in 1991–1994 and recruitment of the 1990–1992 year-classes. Another source of bias is errors in age reading of Baltic cod otoliths (Bagge et al. 1994), with deviations in estimated age of 1–2 years between different countries commonly occurring (ICES 2000). This affects especially the estimation of year-class strength and its interannual variability.

Migration between different areas of the Central Baltic is

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expected to have an impact on the area-disaggregated MSVPA results for all stocks. As stated by ICES (1999*a*), explicit inclusion of the migration process into the MSVPA context is difficult, and at present, no adequate methodology is available. Reliable migration rates are missing for all stocks under consideration, and databases required for the implementation of statistically based spatial multispecies models, e.g., BORMICON (Stefánsson and Pálsson 1998), are not readily available. Even with these databases at hand, however, conflicting output trends depending on considered data sources might also be encountered, as recently demonstrated for the BORMICON application in the Icelandic system (Stefánsson 1998). At present, the only feasible way of resolving spatial distribution in the Baltic is to run a suite of independent MSVPAs for the different subareas, as performed in this study. Following this approach, migration is accounted for by fluctuations in the catch at age data only.

The validation of the area-disaggregated MSVPA results provided several indications of migratory behaviour by cod. The recruitment of cod determined in Subdivisions 26 and 28, in the absence of any reproductive volume, indicates an introduction of recruits from the neighbouring Subdivision 25, the only spawning area at present with hydrographic conditions conducive to egg survival (MacKenzie et al. 2000). Migration between basins was also evidenced from the comparison of relative distribution pattern of age-groups 1 and 2 derived by area-disaggregated MSVPA runs and trawl surveys. The results suggest that most of the recruitment to the eastern spawning areas in the last 10 years has originated in Subdivision 25, as concluded by Bagge and Thurow (1993), juvenile pelagic stages originating in Subdivision 25 being transported to southeastern areas of the Central Baltic and expanding northwards into the Gotland Basin during their second and third years of life. Furthermore, from the comparison of area-disaggregated MSVPA derived relative distributions of adult cod and trawl survey results, it is clear that a substantial part of the adult stock returns to spawn in the Bornholm Basin. Such a spawning migration is confirmed by historical tagging data (Netzel 1974) and catch-per-unit-effort data from commercial fisheries (Lablaika and Lishev 1961). Cod tagged in the vicinity of the Bornholm Basin behaved rather stationary (Bagge et al. 1974). As a consequence, stock numbers at age 1 and 2 in Subdivision 25 are always overestimated by the area-disaggregated MSVPA. This is a problem in modelling cannibalism, as recruits originating from Subdivision 25 growing up in Subdivision 26 are preyed upon in the model by the wrong stock component. However, the adult cod population size was calculated to be of the same order of magnitude in Subdivisions 25 and 26, and thus, it is not expected that predation mortalities are seriously biased.

As a consequence of the observed migration patterns of cod, the application of area-specific results in stock recruitment models depends critically on the behaviour of recruits growing up in Subdivisions 26 and 28 after reaching sexual maturity. If they return to their original spawning ground, independent of the hydrographic situation, no significant influence on area-specific stock–recruitment relationships is to be expected. If, however, favourable hydrographic conditions in eastern basins result in a spawning behaviour close to their nursery areas or if unfavourable spawning conditions force the mature stock components originating from Subdivisions 26 and 28 to migrate to the Bornholm Basin, biased relationships are likely. The first behaviour will result in a gain of recruits in Subdivisions 26 and 28 under favourable oxygen conditions, whereas the latter will lead to a corresponding gain of adults in Subdivision 25 during stagnation periods. In the area-disaggregated MSVPA model, these cod entering the fishery will increase not only the estimated adult stock size in the subdivision but also the estimates of recruitment some years back in time. Although spawning migrations into the Bornholm Basin occur regularly, also in years of favourable environmental spawning conditions in eastern spawning areas (Netzel 1974), the intensity of the spawning migration has been related to environmental conditions (Lablaika and Lishev 1961). Thus, it is likely that both described scenarios occur. Consequently, a certain impact of variable spawning migrations on the population estimates derived by the area-disaggregated MSVPA runs has to be expected. Additionally, separation into subdivisions is not the most appropriate way to distinguish between different spawning populations of cod, as Subdivision 26 contains, in addition to the Gdansk Deep, the southern tip of the Gotland Basin and thus represents to a certain extent a mixture of two spawning stock components.

For sprat, the contribution of Subdivision 25 to the combined stock in the Central Baltic was found to be considerably greater in the MSVPA output than in the September–October hydroacoustic surveys. However, hydroacoustic surveys in May–June showed highest sprat concentrations in the Bornholm Basin, thus confirming the distribution pattern obtained by the area-disaggregated MSVPA runs. This indicates a different distribution of sprat during spawning and feeding periods, potentially caused by migrations between subdivisions, a process that is at present not sufficiently resolved (see Aro 1989; Parmanne et al. 1994). A potential redistribution of the sprat spawning stock during feeding will have an effect on the SSB and recruitment estimated by the area-disaggregated MSVPA runs for the different subdivisions. However, a major part of the catch is obtained during the first half of the year in a fishery directed to prespawning and spawning concentrations (ICES 1999*b*). Hence, the relative distributions derived by the area-disaggregated MSVPA runs and hydroacoustic surveys at spawning time are well in line. Consequently, the effect of migratory behaviour on SSB estimates should be of limited importance.

In summary, the area-disaggregated MSVPA approach presented here has, through comparison with existing data sets, successfully resolved the basin-specific stock dynamics of cod and sprat in the Central Baltic Sea. This result allows the application of the area-disaggregated MSVPA to spatially resolve the SSB of the different spawning basins, thereby allowing the utilisation of area-specific reproductive success in recruitment modelling of these stocks (Köster et al. 2001). This is a key issue in the management of Baltic fish stocks.

Utilisation of basin-specific spawning stock sizes and structures as a measure of the stock's reproductive effort in different spawning areas is to a certain degree affected by migration. However, as the fishery on cod and sprat tradi-

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tionally focuses on prespawning and spawning concentrations, the area-disaggregated MSVPA derived results are believed to give an improved and extended estimate of the time series of stock size, structure, and distribution when compared with available trawl and hydroacoustic survey estimates. Furthermore, the results obtained during this exercise, in conjunction with the available survey information, may be utilised to estimate migration rates between different subareas, an issue affecting the ability of the stocks to optimise suitable spawning habitats when available.

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Appendix

Table A1. SSB (second quarter), recruitment (age-group 1, first quarter), and stock size (cod: age-group 2+, first quarter; herring and sprat: age-group 1+, fourth quarter) in different subdivisions (SD) of the Central Baltic determined from area-disaggregated MSVPA.

	Cod			Herring			Sprat		
Year	SD 25	SD 26	SD 28	SD 25	SD 26	SD 28	SD 25	SD 26	SD 28
SSB (kt)									
1977	92	96	39	387	290	120	93	196	148
1978	96	110	63	384	325	131	82	169	116
1979	105	141	86	376	333	173	55	91	63
1980	110	181	72	343	199	81	26	45	26
1981	144	158	56	293	200	104	19	30	19
1982	135	148	65	261	207	63	29	50	34
1983	163	156	67	339	230	71	69	61	29
1984	118	131	62	312	183	52	161	195	64
1985	116	115	54	277	160	83	218	219	66
1986	87	70	39	273	137	81	223	181	48
1987	87	73	30	227	141	131	210	164	45
1988	88	67	21	225	113	159	199	136	63
1989	76	47	13	206	119	136	164	129	75
1990	79	47	8	195	100	139	239	178	121
1991	54	32	7	159	84	102	330	289	210
1992	41	37	3	170	113	103	469	471	223
1993	88	53	5	164	117	138	585	363	236
1994	116	61	5	198	111	149	569	512	310
1995	110	75	6	187	91	131	421	451	282
1996	113	118	4	179	75	189	417	413	256
Recruitment (millions)									
1977	418	486	242	5532	5 416	2934	10 661	20 896	9 387
1978	327	375	159	6332	4 801	4162	4 910	8 674	5 963
1979	321	316	147	3874	6 860	5955	4 686	21 695	4 561
1980	465	611	235	4930	6 980	6991	3 915	9 565	5 249
1981	500	491	240	9756	12 341	6485	10 137	27 512	17 721
1982	296	281	170	6774	8 166	9928	20 950	14 309	6 191
1983	167	173	128	6558	5 730	8156	38 500	82 162	36 231
1984	146	123	85	5010	4 385	8797	27 486	16 801	10 174
1985	172	128	63	4814	4 086	4953	19 531	14 208	5 930
1986	243	127	67	3594	2 502	3036	14 144	6 939	3 124
1987	145	75	26	3318	2 015	6245	20 239	15 555	10 562
1988	101	40	13	3562	1 757	1616	15 402	3 225	2 924
1989	129	50	18	4645	1 687	2436	30 460	15 867	12 326
1990	65	38	6	3756	2 023	3734	26 584	25 094	13 783
1991	114	53	7	3237	1 921	3458	34 828	36 335	12 566
1992	160	70	7	3647	2 259	2479	36 522	36 327	15 408
1993	112	89	4	2846	1 631	1812	34 879	34 823	20 968
1994	127	170	4	2879	1 567	1776	25 023	20 299	6 382
1995	160	87	6	3788	2 171	2442	80 169	68 414	27 541
1996	168	28	1	3498	1 532	2004	54 916	38 687	18 811

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Table A1 (*concluded*).

	Cod			Herring			Sprat		
Year	SD 25	SD 26	SD 28	SD 25	SD 26	SD 28	SD 25	SD 26	SD 28
Stock size (millions)									
1977	311	363	174	7698	6 227	4959	8 563	22 937	14 762
1978	475	555	289	8049	5 889	5120	5 219	11 290	7 533
1979	541	606	295	6214	5 466	5050	3 498	9 434	3 434
1980	470	579	244	5556	4 625	5554	2 255	4 182	2 669
1981	542	567	232	7415	7 591	5328	4 393	11 982	6 153
1982	629	554	259	7483	8 563	6807	10 059	8 490	3 846
1983	565	478	231	7145	11 147	6238	19 794	41 654	13 065
1984	409	373	185	7064	9 365	7133	25 338	29 829	8 948
1985	292	262	143	6979	4 359	6864	24 358	22 926	7 415
1986	276	197	107	6044	3 620	5920	20 885	16 295	4 977
1987	324	179	90	5685	3 347	8595	24 599	18 540	10 261
1988	304	144	62	5122	2 894	6948	17 559	11 545	8 073
1989	232	94	33	5895	2 850	6080	25 254	18 855	14 349
1990	193	86	26	5840	3 266	7087	32 237	29 792	21 231
1991	143	63	15	6062	3 643	7251	46 885	49 694	25 551
1992	140	82	10	6871	4 300	6458	56 793	62 174	28 336
1993	215	113	12	6617	3 872	5843	61 041	67 892	39 274
1994	239	145	11	6210	3 405	5628	52 004	55 477	33 411
1995	239	228	10	6454	3 314	6004	81 700	77 071	46 772
1996	259	228	10	6391	2 718	5805	76 122	59 937	44 349

Table A2. Indices of stock sizes for different subdivisions (SD): cod age-group 2+ from the Baltic international trawl survey in February–March and age-group 3+ from the Latvian bottom trawl survey in January (left column) and November–December (right column, no.·h^{-1}) and herring and sprat age-group 1+ from international hydroacoustic surveys in September–October (millions).

	Cod age-group 2+			Cod age-group 3+				Herring			Sprat		
Year	SD 25	SD 26	SD 28	SD 26	SD 26	SD 28	SD 28	SD 25	SD 26	SD 28	SD 25	SD 26	SD 28
1977				71		285							
1978				320	405	473							
1979				2830		1068							
1980	663												
1981	1290	1361				908	908						
1982	855	2575	3080	2142	1169	1479	1195	3980	5 290	6 679	4 651	7 383	2 925
1983	891	772	4011	1091	332	2415	1056	4303	6 923	6 652	13 261	22 696	14 536
1984	891	786	1053	3383	734	1428	617	4156	2 881	9 429	7 395	22 405	5 800
1985	884	658	957	1232	288	154	132	2798	3 988	9 350	12 227	9 394	2 178
1986	365	491	539		38	170	83	7696	8 547	7 977	5 647	7 792	3 878
1987	771	694	703	454		42	8	3761	5 172	9 283	4 455	6 120	9 048
1988	479	590	574	332	117	253	65	4725	6 738	6 609	4 917	3 408	3 155
1989	269	226	269	567	72	311	11	3279	6 977	8 745	3 637	36 389	24 143
1990	344	358	182	469		25		6168	8 096	9 823	5 447	8 150	22 656
1991	140	147	201	426		110		4058	10 451	13 408	19 223	46 071	28 498
1992	109	79	27					2977	7 978	9 983	8 084	44 395	28 923
1993	458	172	49										
1994	706	293	68					9037	9 399	16 597	13 983	35 297	24 849
1995	379	928	99					4759	7 421	7 985	18 155	50 214	128 170
1996	489	603	66					7750	4 937	12 821	24 594	62 374	117 462

Note: An empty cell indicates that a reliable survey was not conducted during that period.

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Table A3. Recruitment of cod, herring, and sprat (age-group 1) derived from the Baltic international bottom trawl surveys (no.·h^{-1}) and the international hydroacoustic survey (millions).

	Cod			Herring			Sprat		
Year	SD 25	SD 26	SD 28	SD 25	SD 26	SD 28	SD 25	SD 26	SD 28
1980	10.3								
1981	309.7	3294.6							
1982	26.5	816.2	187.5	768	1146	991	361	2 832	1 037
1983	36.8	52.2	43.8	966	1142	510	7166	15 569	8 610
1984	36.8	309.1	15.4	654	466	3315	581	10 979	1 140
1985	15.0	129.5	11.6	886	713	743	2036	1 415	458
1986	11.9	6.8	5.5	2224	874	261	58	1 127	59
1987	47.7	163.8	6.5	723	1023	1983	306	4 002	5 925
1988	7.7	30.6	9.2	552	510	171	92	44	22
1989	6.4	202.6	10.6	992	745	1230	1010	23 345	7 842
1990	7.9	113.9	8.7	940	1422	1926	339	3 194	4 576
1991	6.0	26.1	0.3	918	1762	1018	2665	26 985	9 254
1992	15.7	10.7	0.1	633	1998	456	636	16 031	12 222
1993	28.7	78.8	2.3						
1994	71.1	227.1	1.7	536	827	277	245	8 955	473
1995	18.4	310.2	0.1	781	952	459	8276	31 382	75 143
1996	2.3	41.7	0.0	373	506	330	3674	24 698	29 674

Note: An empty cell indicates that a reliable survey was not conducted that year.

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Developing Baltic cod recruitment models. II. Incorporation of environmental variability and species interaction

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Abstract: We investigate whether a process-oriented approach based on the results of field, laboratory, and modelling studies can be used to develop a stock–environment–recruitment model for Central Baltic cod (*Gadus morhua*). Based on exploratory statistical analysis, significant variables influencing survival of early life stages and varying systematically among spawning sites were incorporated into stock–recruitment models, first for major cod spawning sites and then combined for the entire Central Baltic. Variables identified included potential egg production by the spawning stock, abiotic conditions affecting survival of eggs, predation by clupeids on eggs, larval transport, and cannibalism. Results showed that recruitment in the most important spawning area, the Bornholm Basin, during 1976–1995 was related to egg production; however, other factors affecting survival of the eggs (oxygen conditions, predation) were also significant and when incorporated explained 69% of the variation in 0-group recruitment. In other spawning areas, variable hydrographic conditions did not allow for regular successful egg development. Hence, relatively simple models proved sufficient to predict recruitment of 0-group cod in these areas, suggesting that key biotic and abiotic processes can be successfully incorporated into recruitment models.

Résumé : Nous cherchons à savoir si une approche axée sur les processus et basée sur des études de terrain, de laboratoire et de modélisation peut servir à développer un modèle stock–milieu–recrutement pour la morue franche (*Gadus morhua*) de la Baltique centrale. À la suite d'une analyse statistique exploratoire, des variables significatives qui influençaient la survie des premiers stades et qui variaient systématiquement d'une site de fraie à un autre ont été incorporées dans des modèles de stock–recrutement, d'abord pour les sites de fraie les plus importants et ensuite combinés pour toute la Baltique centrale. Les variables identifiées comprennent la production potentielle d'oeufs par le stock de géniteurs, les conditions abiotiques qui affectent la survie des oeufs, la prédation des oeufs par les clupéidés, le transport des larves et le cannibalisme. Les résultats indiquent que le recrutement durant la période 1976 à 1995 au site de fraie le plus important, le bassin de Bornholm, était en relation avec la production d'oeufs; cependant, d'autres facteurs significatifs affectaient la survie des oeufs (oxygénation, prédation) et, une fois incorporés, ils expliquaient 69% de la variation dans le recrutement du groupe 0. À d'autres sites de fraie, les conditions hydrographiques variables ne permettaient pas un développement normal et réussi des oeufs. Ainsi, des modèles relativement simples se sont avérés adéquats pour prédire le recrutement des morues du groupe 0 dans ces sites, ce qui laisse croire que des processus dominants abiotiques et biotiques peuvent être incorporés avec succès dans les modèles de recrutement.

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Introduction

Resolving processes driving recruitment variability in fish populations is one of the major challenges facing fisheries scientists and oceanographers (Cushing 1995). For the vast majority of fish stocks, processes causing interannual variations in recruitment remain largely unexplained, resulting in a major source of uncertainty in the management of fish stocks (e.g., defining biological reference points). A number of key processes have been identified as candidates for reducing uncertainty in the prediction of fish stock recruitment. For example, it is now evident that variations in stock structure and condition of the adults can affect the level of egg production (Marshall et al. 1998; Marteinsdottir and

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Thorarinsson 1998; Marshall and Frank 1999) and impact on egg viability and buoyancy. Variations in egg viability and buoyancy influence the survival probability of eggs and larvae (e.g., Kjesbu et al. 1996; Nissling et al. 1998; Trippel 1998) and, combined with variations in stock reproductive effort, are targeted as being responsible for recruitment fluctuations (Marshall et al. 1998; Marteinsdottir and Thorarinsson 1998; Jarre-Teichmann et al. 2000). Furthermore, the effects of predation on fish eggs and larvae (e.g., Bailey and Houde 1989) have the potential to reduce the reproductive success of a stock. Similarly, the loss of eggs and larvae due to transport to suboptimal environments (e.g., Heath and Gallego 1998) can influence recruitment negatively.

In the last 10–15 years, it has been possible to examine many of the major processes currently believed to affect recruitment variability of the cod (*Gadus morhua*) in the Central Baltic (e.g., Bagge and Thurow 1994; MacKenzie et al. 1996). As a result, several new time series are becoming available for variables relating to these processes. In particular, data series have been compiled for egg production (including sex-specific maturity ogives, Tomkiewicz et al. 1997; individual fecundity, Kraus et al. 2000), egg characteristics (buoyancy and viability; Nissling et al. 1998), abiotic factors affecting egg survival (Plikshs et al. 1993; Wieland et al. 1994; MacKenzie et al. 2000), estimates of egg and larval abundances in spawning areas (e.g., Plikshs et al. 1993; Wieland et al. 2000), hydrographic processes affecting larval and 0-group distribution (Voss et al. 1999; Hinrichsen et al. 2001), predation on early life history stages (Köster and Möllmann 2000*a*), and cannibalism (Sparholt 1996; Neuenfeldt and Köster 2000).

It is of interest, therefore, to use this material to investigate whether a process-oriented recruitment model can be developed and to identify what information might be lacking to make such a model reliable. Our approach attempts to follow the success of a year-class during ontogeny from spawner abundance through the egg and larval to the juvenile stage according to Paulik's (1973) framework for examining the entire life history process, a concept broadly accepted but not really implemented yet (Rothschild 2000).

Materials and methods

Stock–recruitment relationships are constructed for different subdivisions of the Central Baltic Sea (see code of International Council for the Exploration of the Sea (ICES)) containing spawning areas with distinct hydrographic regimes (MacKenzie et al. 2000), recruitment success, and stock development trends (Sparholt and Tomkiewicz 2000). The variability in stock–recruitment relationships has been established based on area-disaggregated multispecies virtual population analysis (MSVPA) (Köster et al. 2001). Here, we extend this exercise to investigate the potential environmental processes affecting reproductive success. Environmental variables included are listed in Table 1 and are described in detail below. Based on time series of these variables identified to have a significant impact on production or survival rates of the various life stages, stock–recruitment models are constructed for Subdivisions 25, 26, and 28 containing the major cod spawning areas of the Bornholm Basin, Gdansk Deep, and Gotland Basin. Stock–recruitment models having the highest predictive power were then utilised to establish a combined stock and recruitment model for the entire Central Baltic by integrating predicted values over the different subdivisions.

Spawning stock size and distribution

Spawning stock abundance and biomass estimates for Subdivisions 25, 26, and 28 were obtained by performing area-disaggregated MSVPA runs for the period 1977–1996 (Köster et al. 2001). In order to extend the time series to include 1976, a year with well above average reproductive success, the MSVPA abundance estimates were extrapolated backwards. This was achieved by assuming the same age-specific natural mortalities in 1976 as in 1977, applying absolute fishing mortality rates derived for 1976 by the regular stock assessment (ICES 1997) and relative quarterly fishing mortalities as determined by the area-disaggregated MSVPA runs for 1977.

Recruitment

Recruitment estimates for ages 0 and 1 in the different subdivisions were derived by area-disaggregated MSVPA runs (Köster et al. 2001). It should be noted that estimates of recruitment in 1996 were omitted from the analysis, as they are heavily dependent on the tuning performed. Alternative area-specific recruitment indices of age-group 1 were utilised for validation of model output. These were derived by CORE (1998) from international bottom trawl surveys conducted since 1982 (Sparholt and Tomkiewicz 2000).

Potential egg production

To estimate the basin-specific seasonal egg production by the spawning stock, first, sex ratios and female maturity ogives were applied to basin-specific population abundances according to age derived by area-disaggregated MSVPA runs. Annual sex ratios and proportions of sexually mature individuals were utilised for Subdivision 25 in 1986–1996 and for Subdivision 26 in 1993–1996; otherwise, 5-year averages were used (Tomkiewicz et al. 1997). Revised estimates of basin- and sex-specific spawning stock biomass (SSB) were coupled to a time series of average relative fecundity values, i.e., individual fecundity per unit of total body weight (Shapiro 1988; Bleil and Oeberst 1996; Kraus et al. 2000), to estimate the annual potential egg production (Appendix Tables A1 and A2). Missing information (Table 1) was derived by linear interpolation. The applied procedure was enabled by the observation that relative fecundity in Baltic cod is independent of body size (Kraus et al. 2000). It should be noted that a significant variability in relative fecundity was detected between years but not between spawning areas within a specific year (Kraus et al. 2000); hence, relative fecundity was assumed to be similar among areas.

Observed egg and larval standing stocks and production

Mean annual egg and larval abundance values are available for the different subdivisions from ichthyoplankton surveys in 1976–1996 (Appendix Tables A1 and A2) based on data compiled by Karasiova (1995), E.M. Karasiova (Atlantic Scientific Research Institute of Marine Fisheries and Oceanography, Kaliningrad, Russia, personal communication), MacKenzie et al. (1996), Makarchouk (1997), A. Makarchouk (Latvian Fisheries Research Institute, Riga, Latvia, personal communication), R. Voss (Institute of Marine Sciences, Kiel, Germany, personal communication), and Wieland et al. (2000). Egg abundance estimates are based on a 3-month period encompassing the main spawning period, i.e., April–June up to 1989 and successively shifted to May–June (1990–1992) and June–August (1993–1996) to take into account a shift in the spawning period in recent years (Wieland et al. 2000). A more detailed estimate of daily egg production rates was utilised for the Bornholm Basin based on ichthyoplankton surveys performed from 1986 to 1996 (Appendix Table A1). Estimates of abundance were

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Table 1. Variables incorporated into the statistical exploratory analysis and subsequent recruitment modelling, information on methodology, time periods and areas covered as well as data sources.

Variable	Basis	Time period	Subdivision(s)	Source of time series
Potential egg production	Stock numbers from MSVPA	1977–1996	25, 26, 28	Köster et al. 2001
	Sex ratios, maturity ogives	1980–1996	25, 26, 28	Tomkiewicz et al. 1997
	Average relative fecundity	1976–1978, 1983–1984	26, 28	Shapiro 1988
		1987–1992, 1995–1996	25, 26	Kraus et al. 2000
		1994	25	Bleil and Oeberst 1996
Egg and larval abundance	Ichthyoplankton surveys	1994–1996	26	Karasiova 1995; E.M. Karasiova, unpublished data
		1976–1985	25	MacKenzie et al. 1996
		1991–1996	26, 28	Makarchouk 1997; A. Makarchouk, unpublished data
		1976–1990	26, 28	Plikshs et al. 1993
		1986–1996	25	Wieland et al. 2000; R. Voss, unpublished data
Oxygen-related egg survival	Vertical distribution of eggs in relation to density	1986–1996	25	This study, based on Wieland and Jarre-Teichmann 1997
	Experiments on viable hatch		25, 26	Wieland et al. 1994; Rohlf 1999
Egg consumption by clupeids	Cod egg consumption rates	1988–1996	25	Köster and Möllmann 2000*a*
	Predator populations	1976–1996	25	Köster and Möllmann 2000*b*; Köster et al. 2001
	Vertical predator–prey overlap	1976–1996	25	This study, based on above information
Larval transport index	Cumulative wind energy	1976–1996	25	Jarre-Teichmann et al. 2000
	Direction of transport dependent on wind forcing	1976–1996	25	This study, based on model runs (Hinrichsen et al. 2001)
Cannibalism rates of juveniles	MSVPA	1977–1996	25, 26, 28	Köster et al. 2001
Recruitment age 1	Bottom trawl survey	1980–1996	25, 26, 28	CORE 1998

Note: See text for addresses of authors of unpublished data.

obtained based on egg stage (Thompson and Riley 1981) specific abundance data and egg development – temperature relationships (Wieland et al. 1994). Temperatures at the depth of the centre of mass of eggs were utilised for the estimation of developmental period. These were obtained from CTD (conductivity–temperature–depth) casts performed concurrently with the vertically resolving ichthyoplankton sampling (Wieland and Jarre-Teichmann 1997). Finally, daily egg production rates were calculated by dividing the stage-specific abundance of live eggs by the development time of each egg stage. Larval abundance data refer to a period similar to the 3-month period of egg abundance estimates but shifted to account for the 2- to 4-week period of development from egg to larvae (Wieland et al. 1994).

Impact of oxygen concentration on egg survival

Estimates of the "reproductive volume," i.e., the volume of water suitable for successful egg development (Plikshs et al. 1993), in the different subdivisions were obtained from MacKenzie et al. (2000) for the peak spawning periods (Appendix Tables A1 and A2). However, for the Bornholm Basin, two modifications of this index were performed based on the suitability of the spawning volume for successful egg development.

The first modification was based on the oxygen conditions within the salinity range over which cod eggs are neutrally buoyant, giving a measure of the quality of the reproductive volume for successful development of cod eggs (Appendix Table A1). This modification is based on an integration of the mean oxygen concentrations per 1-m depth interval over the thickness of the spawning layer using stations similar to those employed in the original calculation of the spawning volume (MacKenzie et al. 2000).

For the second modification, the fraction of the egg production surviving in each year (Appendix Table A1) was estimated based on (*i*) the predicted vertical distribution of cod eggs in 5-m depth intervals relative to water density (see below), (*ii*) the oxygen concentration measured at each depth interval, and (*iii*) an oxygen concentration – cod egg survival relationship derived from laboratory experiments (Wieland et al. 1994) with percent survival up to the end of the yolk-sac phase (v) given by

$$v = -0.5689 + 0.3368 \times O_2 - 0.0173 \times O_2^2 \quad (n = 15,\ r^2 = 0.94)$$

where O_2 is the oxygen concentration at depth of incubation (Rohlf 1999). To model the vertical distribution of eggs, the observed distribution of the youngest egg stage (IA) obtained from vertically resolving ichthyoplankton sampling in 1986–1996 (Wieland and Jarre-Teichmann 1997) was examined in relation to water density profiles by fitting a parabolic function to the log relative distribution data (IA):

$$\ln(IA_z) = a + b \times \rho_z + c \times \rho_z^2$$

where ρ_z is the water density at depth interval z. However, cod eggs become less buoyant after inflows when higher salinity occurs in the bottom water (Wieland and Jarre-Teichmann 1997). Hence, these hydrographic situations were modelled separately. In order to adjust for this change in buoyancy, we defined inflow situations in

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the Bornholm Basin by the depth at which the oxygen concentration reached 2 mL·L^{-1} (inflow >85 m) and by the average salinity within the reproductive volume (inflow salinity >13.5 psu). Furthermore, upon inspection of the data, a seasonal effect in the vertical distribution of cod eggs was detected. Hence, the following hydrographic and spawning situations were defined to group the data: (*i*) stagnation/early spawning, (*ii*) stagnation/late spawning, (*iii*) inflow/early spawning, and (*iv*) inflow/late spawning. The fitted parabolic functions explain between 69 and 80% of the variance in the relative vertical distribution of cod eggs.

Predation on cod eggs by clupeids

Consumption of cod eggs by sprat (*Sprattus sprattus*) has a significant impact on egg survival in the Bornholm Basin in spring and early summer, while later in the cod spawning season, herring (*Clupea harengus*) replaces sprat as the principal predator (Köster and Möllmann 2000*a*). Predation pressure by sprat decreased throughout the 1990s, while the impact of herring increased (Köster and Möllmann 2000*a*), due to a delay in spawning of cod (Wieland et al. 2000). Apart from intra- and interannual trends, spatial variation in the intensity of egg predation occurs, with consumption in the Gdansk Deep and Gotland Basin being considerably lower than in the Bornholm Basin. This difference has been attributed to (*i*) the lack of light for successful feeding on the transparent and motionless cod eggs at the increased depth of occurrence in these eastern spawning basins caused by lower salinity within and below the halocline (Geldmacher 1998) and (*ii*) a related limited vertical overlap between cod eggs and their clupeid predators (CORE 1998). Thus, predation on cod eggs by clupeids was included as a parameter in the model only in Subdivision 25.

Köster and Möllmann (2000*a*) found that low oxygen concentration in the bottom water limited the vertical distribution of clupeids during the daylight feeding period, while the density regime determined the vertical distribution of cod eggs. Based on these observations, the average capture depth of the clupeids (Köster and Möllmann 2000*a*) and the average depth in which highest concentrations of cod eggs occurred (Wieland and Jarre-Teichmann 1997) were combined into an index of vertical predator–prey overlap determined for sampling dates in 1990–1996. Assuming an average residence depth of clupeids to correspond to the depth of occurrence of an oxygen concentration of 2 mL·L^{-1}, corrected by an offset of 3 m as observed in 1990–1996, allowed, in combination with observed (1986–1989) and modelled vertical distributions of cod eggs (1976–1985), the calculation of predator–prey overlap indices for the entire time series. In inflow situations, when oxygenated water occurred over the whole water column, the maximum average depth of capture encountered in 1994, a year when anoxic conditions did not exist in the basin, was utilised as dwelling depths of clupeids. Applying a linear relationship between the ratio of hourly consumption and egg abundance with the vertical predator–prey overlap index (n = 8; sprat: r^2 = 0.77, herring: r^2 = 0.42) enabled the prediction of consumption rates by predator populations (Köster and Möllmann 2000*b*) for the main spawning periods in May 1976–1992. For the period from 1993 on, characterised by late cod spawning activity (Wieland et al. 2000), the mean observed consumption relative to cod egg availability was utilised. Predation pressure was introduced into the analysis as a relative index expressed as consumption per standing stock of eggs (Appendix Table A1) scaled to the potential egg production, setting the maximum predation pressure to result in a 95% egg removal. This approach allowed inclusion of predation on eggs into the time series by subtracting the amount consumed from the amount produced.

Larval retention and transport

Jarre-Teichmann et al. (2000) demonstrated that the cumulative wind energy at peak spawning time impacts on cod recruitment success, the suggested process being a transport of larvae and pelagic juveniles to coastal nursery habitats favourable for recruitment during periods of high wind energy and a retention in the central basins during periods of low wind stress of variable wind direction (Hinrichsen et al. 2001).

To incorporate these transport processes into our exploratory analysis, the cumulative wind energy as utilised by Jarre-Teichmann et al. (2000) was modified. The starting point for the integration of wind energy was set to the annual date of peak larval abundance assuming a larval drift period of 45 days. Studies by Voss et al. (1999) and Hinrichsen et al. (2001) demonstrated that larval drift towards the west and north is caused primarily by winds of westerly and southerly direction, whereas winds of opposite direction result in larval transport to the south and east. Periods of transport identified are those in which sufficient wind energy occurs during 45 days (or less) after hatch to transport more than 50% of the hatched larvae to the northern or southern coastal environments of the Bornholm Basin (<30 m water depths). Periods of lower wind energy are defined as periods of retention. Thus, differences in cumulative wind energy between winds coming from the southern to western direction (defined as positive cumulative wind energy differences) and northern to eastern direction (negative differences) were calculated and converted into a relative frequency of occurrence of larval transport from the spawning ground towards coastal environments (Appendix Table A1). Wind energy was derived from a wind data time series at Christiansø (CORE 1998). The relative frequencies of larval occurrence within different coastal environments are based on results of hydrodynamic scenario modelling analysing drift patterns associated with wind forcing of different direction (Hinrichsen et al. 2001).

Cannibalism within the 0-group stage

Cannibalism has been implicated as an important density-dependent mechanism influencing Baltic cod recruitment success (Sparholt 1996). Estimates of cannibalism on 0-group cod are available for the time series from area-disaggregated MSVPA runs (Köster et al. 2001). These mortality rates can be utilised to estimate age-group 1 recruitment from 0-group abundance predicted by established stock–recruitment models, applying a residual mortality of 0.2·year^{-1}. However, in order to construct predictive models of recruitment at age 1 beyond the time period covered by the MSVPA, we related mortality due to cannibalism linearly to the adult biomass. This procedure has been suggested by ICES (1993) for herring and sprat as prey for cod.

Model construction and validation

The basis for developing stock–recruitment relationships for Baltic cod based on environmental and spatial heterogeneity is the identification of causal relationships between survival rates of different early and juvenile life stages, environmental factors, and species interactions. In order to do so, simple and multiple linear regression techniques were applied to the complete data series from 1976 to 1996 and a more extensive subset of these data available for Subdivision 25 from 1986 to 1995. Based on the resulting significant variables, stock–recruitment models with combinations of different factors were constructed for Subdivisions 25, 26, and 28 and subsequently combined for the entire Central Baltic.

The parameters of the area-specific models are based on the entire time series of data available. However, in order to obtain an indication of the sensitivity of parameter estimates for model configurations having the best predictive capabilities and to evaluate the accuracy of model predictions for time periods not represented by the model, the first 4 and 5 years of data, i.e., years with high reproductive success, were excluded and the models refitted utilising only data sets 1979–1995 and 1980–1995 for parameter estimation. Predictions from the refitted models were then compared with

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observations for 1976 to 1979–1980. A similar test was performed for the periods 1991–1992 to 1995 utilising data subsets covering the periods 1976–1990 and 1976–1991 in order to establish whether the models are able to reproduce the increase in recruitment, which followed increased inflow activity since 1991 and especially the last major Baltic inflow in early 1993 (Matthäus and Lass 1995). As a further validation of the model, predicted 0-group abundance and cannibalism rates acting on 0-group were utilised to predict recruitment at age 1 and compared with corresponding area-specific recruitment indices obtained from international bottom trawl surveys (Sparholt and Tomkiewicz 2000).

Results

Explaining variability in stock–recruitment relationships

Survival during the egg stage

The two primary mechanisms influencing cod egg survival in Subdivision 25 are predation by clupeids and the oxygen conditions at the depth of incubation. In order to examine the effects of these processes on egg survival, the daily production of egg stage III from ichthyoplankton surveys was related to the potential egg production. Egg production at stage III was utilised as a proxy for the production of the oldest egg stage IV, as the abundance of this stage is highly variable due to a relatively short stage duration and hatching, which in Baltic cod already commences at this stage (Wieland et al. 1994). Justification for the use of potential egg production as an estimate of the reproductive effort is based on a high correlation between the production estimates of stage IA cod eggs from ichthyoplankton surveys and potential egg production (statistical model 1, $r^2 = 0.74$). Coefficients and significance levels as well as Durbin Watson statistics are given in Table 2 for each regression analysis performed. A linear regression of the egg survival up to stage III versus the oxygen-related egg survival (model 2, $p = 0.04$) explains 39% of the variance encountered, with a high positive residual in 1994 and negative residuals observed in 1995 and 1996 (Fig. 1*a*). Utilising the egg consumption index, a negative linear relationship (model 3, $p = 0.09$) explained 29% of the variance in egg survival until stage III (Fig. 1*b*). Incorporating both processes into the potential egg production (i.e., subtracting the consumed eggs and multiplying by the oxygen-related relative survival) revealed a significant linear regression (model 5, $p = 0.003$) with egg production at stage III ($r^2 = 0.66$). However, the potential egg production explained 53% of the variance alone (model 4). Again, difficulties in explaining values in recent years occurred, especially in 1994 (Fig. 1*c*). Excluding 1994 from the regression analysis increased the explained variance to 83% (model 6).

For Subdivisions 26 and 28, linear regressions of observed egg abundance values versus the potential egg production revealed a significant relationship ($p = 0.012$) only for Subdivision 28 (models 26 and 27, Table 3). However, a time trend in the residuals was obvious, with high positive residuals in the beginning of the time series, i.e., up to 1980, and primarily negative residuals thereafter. Since the beginning of the 1980s, egg abundance was less than expected from the available SSB, an observation explained by the occurrence of unfavourable oxygen conditions resulting in extremely high egg mortality. This is confirmed when observed egg abundance versus potential egg production is regressed on the reproductive volume, yielding significant relationships for both areas (model 28, $p < 0.001$; model 29, $p = 0001$), explaining 55 and 44% of the variance encountered, respectively (Table 3).

Survival until the larval stage

Linear regressions of the ratio of larval abundance to potential egg production, as a measure of survival to the larval stage, versus the oxygen-related egg survival as well as the consumption index revealed no significant relationships for Subdivision 25 (models 7 and 8, Table 2). Replacing the oxygen-related egg survival with the oxygen content in the reproductive volume revealed an improved, but still only weak relationship (model 9, $r^2 = 0.15$), while a significant relationship was derived for the larval abundance versus the potential egg production (model 10, $p = 0.026$). However, the relationship still explains only 23% of the variance encountered (Fig. 2*a*). A significant linear relationship of larval abundance per unit of egg production at stage III versus the oxygen-related egg survival as well as the predation index was found (model 11 and 12), but with a negative relationship for the oxygen impact and a positive one for the predation. The statistical models indicate a reduction in larval survival with increasing reproductive volume and decreasing egg predation pressure, both relationships being biologically not reasonable. There is also no direct relationship between larval abundance and egg production at stage III (model 13). The only sensible statistical model derived by the exploratory analyses is a multiple linear regression including potential egg production corrected for egg consumption ($p = 0.085$) and the oxygen content in the reproductive volume ($p = 0.062$) as independent variables (model 14). The model explained 31% of the variance in the larval abundance. The time series of observed and predicted values (Fig. 2*b*) clearly demonstrate that the model was unable to explain high larval abundances in 1980 and 1981 and resulted in negative residuals from 1992 to 1996. It should be noted that a significant autocorrelation in the residuals occurred (Table 2).

For Subdivisions 26 and 28, the larval abundance per unit of potential egg production was significantly related to the reproductive volumes (model 30, $r^2 = 0.58$; model 31, $r^2 = 0.41$) (Table 3). Although these relationships show high variability in the survival to the larval stage, intermediate to high reproductive volumes obviously have an impact on survival until the larval stage. An anomalous situation was encountered in 1994, as no larvae were observed in either area, despite the existence of a fairly high reproductive volume.

Survival from the larval to the 0-group stage

Recruitment at age 0 in Subdivision 25 was higher when larvae were more abundant (model 15, $r^2 = 0.65$) (Fig. 3*a*). The significant intercept of the relationship is primarily caused by recruitment observations originating from very low larval abundance values in 1992–1993 and 1995. These low abundances resulted in extremely high ratios of recruitment at age 0 to larval abundance, pointing to a problem in the larval abundance data in the most recent years. Comparing the ratio of recruitment at age 0 to larval abundance, as a measure of larval survival, with the oxygen content in the reproductive volume or the larval transport index did not

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Table 2. Results of exploratory analyses and stock–recruitment relationships for Subdivision 25: parameter estimates and their significance levels, r^2 values, and Durbin Watson (DW) statistics indicating serial correlation in residuals.

Model	Dependent variable	Time series	Independent variable	Parameter estimate	p	r^2	DW
1	Egg production stage IA	1986–1996	Intercept	-2.42×10^{10}	0.089		
			Potential egg production	2.80×10^{-3}	0.001	0.74	1.30
2	Ratio egg production stage III to potential egg production	1986–1996	Intercept	5.53×10^{-5}	0.156		
			Oxygen-related survival	2.08×10^{-4}	0.040	0.39	2.30
3		1986–1996	Intercept	1.88×10^{-4}	0.001		
			Egg consumption index	-4.77×10^{-4}	0.088	0.29	2.70
4	Egg production stage III	1986–1996	Intercept	-1.08×10^{9}	0.453		
			Potential egg production	1.89×10^{-4}	0.011	0.53	1.98
5		1986–1996	Intercept	9.67×10^{8}	0.206		
			Potential egg production corrected for egg survival	3.15×10^{-4}	0.003	0.66	2.38
6		1986–1996	Intercept	1.34×10^{9}	<0.001		
		Without 1994	Potential egg production corrected for egg survival	1.54×10^{-4}	<0.001	0.83	1.98
7	Ratio larval abundance to potential egg production	1976–1996	Intercept	1.13×10^{-3}	0.031		
			Oxygen-related survival	2.00×10^{-4}	0.833	<0.01	1.45
8		1976–1996	Intercept	1.21×10^{-3}	0.002		
			Egg consumption index	1.92×10^{-4}	0.958	<0.01	1.49
9		1976–1996	Intercept	6.86×10^{-4}	0.071		
			Oxygen content in reproductive volume	7.10×10^{-6}	0.084	0.15	1.21
10	Larval abundance	1976–1996	Intercept	1.39×10^{9}	0.935		
			Potential egg production	1.15×10^{-3}	0.026	0.23	1.06*
11	Ratio larval abundance to egg production stage III	1986–1996	Intercept	20.20	0.007		
			Oxygen survival factor	−29.10	0.068	0.32	2.12
12		1986–1996	Intercept	0.26	0.963		
			Egg consumption index	76.30	0.071	0.32	2.62
13	Larval abundance	1986–1996	Intercept	1.77×10^{10}	0.051		
			Egg production stage III	−0.073	0.972	<0.01	1.43
14		1976–1996	Intercept	-2.23×10^{9}	0.873		
			Potential egg production – egg predation	2.39×10^{8}	0.085	0.38	
			Oxygen content in reproductive volume	9.12×10^{-4}	0.062	Adj. 0.31	0.74*
15	Recruitment at age 0	1976–1995	Intercept	1.43×10^{8}	0.004		
			Larval abundance	4.70×10^{-3}	<0.001	0.65	0.99*
16	Ratio recruitment at age 0 to larval abundance	1976–1991	Intercept	0.010	0.001		
			Oxygen content in reproductive volume	-1.16×10^{-5}	0.625	0.02	1.73
17		1976–1991	Intercept	9.78×10^{-3}	<0.001		
			Larval transport index	-6.41×10^{-5}	0.586	0.02	1.75
18	Recruitment at age 0	1976–1995	Intercept	9.51×10^{7}	0.074		
			Larval abundance	3.97×10^{-3}	<0.001	0.70	
			Oxygen content in reproductive volume	9.96×10^{5}	0.106	Adj. 0.66	1.39
19		1976–1995	Intercept	1.07×10^{8}	0.067		
			Larval abundance	3.83×10^{-3}	<0.001		
			Oxygen content in reproductive volume	1.09×10^{6}	0.095	0.70	
			Larval transport index	-9.55×10^{5}	0.549	Adj. 0.65	1.45
20	Predation mortality at age 0	1977–1996	Intercept	7.74×10^{-3}	0.874		
			SSB	3.08×10^{-9}	<0.001	0.68	1.55
21	Recruitment at age 0	1976–1995	Intercept	1.89×10^{7}	0.747		
			Potential egg production – egg predation	8.39×10^{-6}	<0.001	0.69	
			Oxygen content in reproductive volume	1.39×10^{6}	0.022	Adj. 0.66	0.96*
22		1976–1995	Intercept	4.40×10^{7}	0.452		
			Potential egg production – egg predation	8.34×10^{-6}	<0.001		

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Table 2 (*concluded*).

Model	Dependent variable	Time series	Independent variable	Parameter estimate	p	r^2	DW
			Oxygen content in reproductive volume	1.51×10^6	0.012	0.74	
			Larval transport index	-2.36×10^6	0.118	Adj. 0.69	1.38
23		1976–1995	Intercept	3.77×10^7	0.370		
		Without 1979	Potential egg production – egg predation	7.52×10^{-6}	<0.001		
			Oxygen content in reproductive volume	1.56×10^6	0.001	0.84	
			Larval transport index	-1.80×10^6	0.105	Adj. 0.80	1.28
24	ln(recruitment at age 0)	1976–1995	Intercept	6.56	0.016	0.70	0.74*
			ln(potential egg production – egg predation)	0.398	<0.001	Adj. 0.66	
			ln(oxygen in reproductive volume)	0.188	0.155		
25		1976–1995	Intercept	6.97	0.010	0.74	0.94*
			ln(potential egg production – egg predation)	0.384	<0.001	Adj. 0.69	
			ln(oxygen in reproductive volume)	0.223	0.091		
			ln(larval transport index)	–0.084	0.151		

Note: *Significant at 5% level.

reveal significant relationships, even when removing years after 1991 from the analysis (models 16 and 17). Nevertheless, including the oxygen content in the reproductive volume in a multiple linear regression, assuming that oxygen concentration impacts on survival of early larvae found within and below the halocline (Grønkjær and Wieland 1997), resulted only in a slightly better fit of the recruitment to larval abundance relationship (model 18), with the significance level of the regression coefficient being $p = 0.106$. Including the larval transport index as a variable did not increase the explained variance or remove the significant positive intercept (model 19). However, the intercept becomes insignificant if the last 4 years of data are omitted from the model fitting.

A linear regression of the recruitment at age 0 on larval abundance (Fig. 3*b*) for Subdivision 26 explains less variability than in Subdivision 25 (model 32, $r^2 = 0.40$) but is, however, still significant ($p = 0.003$). In contrast, the corresponding relationship for Subdivision 28 is not significant (model 33), with a rather high number of zero observations and a large scatter observed in the remaining data points (Fig. 3*c*). As in Subdivision 25, significant positive intercepts were encountered in both areas, i.e., even with no larvae obtained in the ichthyoplankton surveys, recruitment regularly occurred.

Cannibalism within the 0-group stage

Predation mortality rates of 0-group cod are linearly related to the SSB of cod as determined by the MSVPA runs (Fig. 4). The relationships are highly significant in all areas under consideration (models 20, 34, and 35, $p < 0.001$ in all cases, $r^2 = 0.68$–0.82).

Stock–recruitment relationships including environmental factors and species interaction

Based on significant variables identified in the exploratory analysis (potential egg production corrected for the removal by egg predation and the oxygen content in the reproductive volume), a multiple regression based stock–recruitment relationship was developed for Subdivision 25 (model 21, Fig. 5*a*). The statistical model explained 66% of the variance encountered, with both regression coefficients being significant ($p < 0.001$ and $p = 0.022$). However, a significant autocorrelation was observed in the residuals (Fig. 5*c*). The statistical model developed showed high deviations from observed values in 1979 (positive residuals) as well as in 1984, 1993, and 1994 (negative residuals). Incorporating the larval transport index as an additional variable improved model 23 ($r^2 = 0.69$) (Fig. 5*b*), with the regression coefficient being nearly significant and the autocorrelation of the residuals being no longer significant (Fig. 5*c*).

As recruitment at age 0 is lognormally rather than normally distributed (Shapiro–Wilks test), a multiplicative model was established by natural logarithm (ln) transforming the dependent and independent variables. The simpler model 24, without the larval transport index as a variable, also explained 66% of the variance (Fig. 6*a*); however, the regression coefficient for the logarithmic sum of oxygen concentration in the reproductive volume was not significant, contrary to the other coefficient (Table 2). Deviations between observations and predicted values were especially obvious for the beginning of the time series until 1981, where the model underestimated recruitment, while in the most recent years (1993–1995), the model overestimated recruitment. Residuals were significantly autocorrelated (Fig. 6*c*). Including the larval transport index as an additional variable (Fig. 6*b*) increased the explained variance (model 25, $r^2 = 0.69$). However, the regression coefficient for the transformed transport index was not significant ($p = 0.151$) either, and again, the relationship was negative. The behaviour of the model with respect to time trends and autocorrelation in residuals was similar to that described for the simpler model 24.

In Subdivision 26, potential egg production and the repro-

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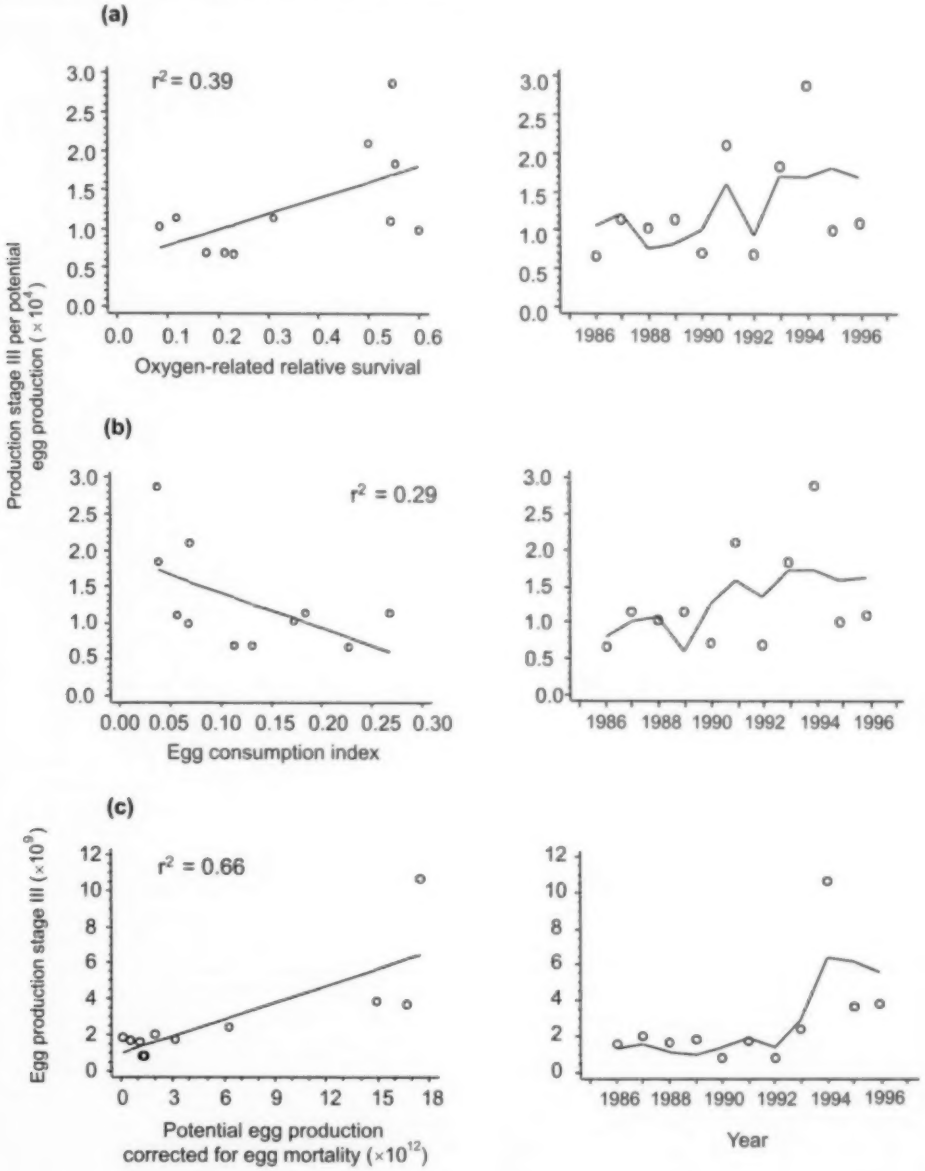
Fig. 1. Linear regressions of daily cod egg production at stage III in Subdivision 25 per unit of egg potential production (as a measure of egg survival) on (*a*) oxygen-related relative egg survival (see model 2) and (*b*) an index of egg consumption (see model 3) and (*c*) linear regression of daily egg production at stage III on potential egg production corrected for oxygen-related mortality and consumption (model 5). Circles, observed values; lines, predicted values.



ductive volume were utilised in a multiple linear regression (model 36) that explained 55% of the variance in recruitment at age 0 (Fig. 7*a*). Both regression coefficients were significant ($p = 0.005$ and $p = 0.032$), and no autocorrelation was indicated. A large positive deviation between observed and predicted recruitment occurred in 1979, with relatively small negative residuals encountered throughout the period 1982–1988. The corresponding logarithmic model 40 fitted the data better (Fig. 7*b*), with an explained variance of 61%, but again, an underestimation of recruitment at the beginning of the time series as well as autocorrelation of residuals was apparent (Fig. 7*c*).

Models 38 and 41 for Subdivision 28 explained 66% and 78% of the variance in recruitment and ln(recruitment), respectively (Figs. 8*a* and 8*b*). In the multiplicative model, the regression coefficient of the reproductive volume was not significant, and residuals again showed a time trend and were also significantly autocorrelated at a time lag of 1 year

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Table 3. Results of exploratory analyses and stock–recruitment relationships for Subdivisions 26 and 28: parameter estimates and their significance levels, r^2 values, and Durbin Watson (DW) statistics indicating serial correlation in residuals.

Model	Dependent variable	Subdivision	Time series	Independent variable	Parameter estimate	p	r^2	DW
26	Egg abundance	26	1976–1996	Intercept	1.64×10^{10}	0.903		
				Potential egg production	6.19×10^{-3}	0.106	0.13	0.59*
27		28	1976–1996	Intercept	2.82×10^{10}	0.813		
				Potential egg production	1.18×10^{-2}	0.012	0.29	2.07
28	Ratio of egg abundance to potential egg production	26	1976–1996	Intercept	3.18×10^{-3}	0.853		
				Reproductive volume	1.10×10^{-3}	<0.001	0.55	1.34
29		28	1976–1996	Intercept	7.65×10^{-3}	0.005		
				Reproductive volume	1.50×10^{-4}	0.001	0.44	2.11
30	Ratio of larval abundance to potential egg production	26	1976–1996	Intercept	5.56×10^{-6}	0.950		
				Reproductive volume	1.30×10^{-5}	<0.001	0.58	1.26
31		28	1976–1996	Intercept	4.87×10^{-4}	0.400		
				Reproductive volume	3.26×10^{-5}	0.002	0.41	1.69
32	Recruitment at age 0	26	1976–1995	Intercept	1.95×10^{8}	0.044		
				Larval abundance	7.80×10^{-3}	0.003	0.40	1.25
33		28	1976–1995	Intercept	1.32×10^{8}	0.009		
				Larval abundance	7.67×10^{-4}	0.150	0.11	0.55*
34	Predation mortality at age 0	26	1977–1996	Intercept	–0.115	0.095		
				SSB	5.64×10^{-9}	<0.001	0.82	2.56
35		28	1977–1996	Intercept	–0.049	0.381		
				SSB	1.09×10^{-8}	<0.001	0.82	1.65
36	Recruitment at age 0	26	1976–1995	Intercept	-7.40×10^{7}	0.523		
				Potential egg production	1.08×10^{-5}	0.005	0.60	
				Reproductive volume	2.78×10^{6}	0.032	Adj. 0.55	1.40
37		26	1976–1995	Intercept	-6.68×10^{7}	0.159		
			Without 1979	Potential egg production	8.31×10^{-6}	<0.001	0.89	
				Reproductive volume	3.05×10^{6}	<0.001	Adj. 0.87	1.19
38		28	1976–1995	Intercept	-3.59×10^{7}	0.383		
				Potential egg production	8.18×10^{-6}	<0.001	0.70	
				Reproductive volume	7.45×10^{5}	0.088	Adj. 0.66	1.47
39		28	1976–1995	Intercept	-2.68×10^{7}	0.486		
			Without 1979	Potential egg production	7.24×10^{-6}	<0.001	0.67	
				Reproductive volume	7.83×10^{5}	0.058	Adj. 0.63	1.42
40	ln(recruitment at age 0)	26	1976–1995	Intercept	–5.44	0.467		
				ln(potential egg production)	0.792	0.004	0.65	
				ln(reproductive volume[a])	0.142	0.044	Adj. 0.61	0.80*
41		28	1976–1995	Intercept	–18.00	0.001		
				ln(potential egg production)	1.190	<0.001	0.81	
				ln(reproductive volume[a])	0.115	0.137	Adj. 0.78	0.79*

Note: *Significant at 5% level.
[a]A constant unity of 0.1 was added before ln transformation.

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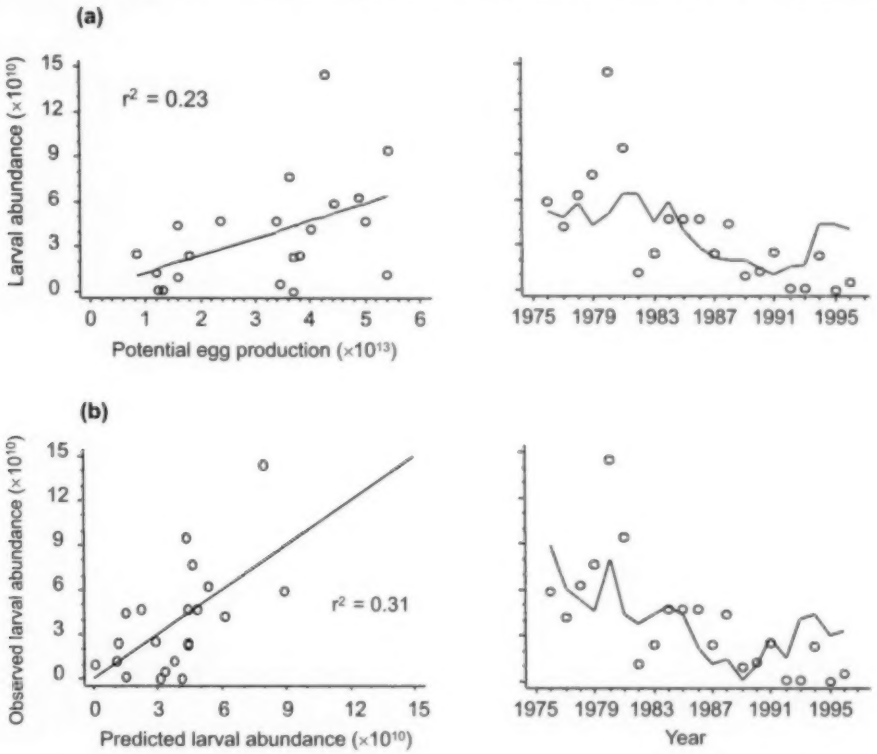
Fig. 2. Linear regressions of cod (*a*) larval abundance on potential egg production in Subdivision 25 (see model 10) and (*b*) observed larval abundance from ichthyoplankton surveys and predicted by a multiple linear regression (model 14) utilising potential egg production and oxygen content in the reproductive volume as independent variables. Circles, observed values; lines, predicted values.



(Fig. 8*c*). Although the time trend in residuals is less pronounced in the additive model, considerable positive residuals occurred in 1976 and 1979 and negative residuals in 1984–1985.

The sum of the area-specific predicted recruitment at age 0 from the additive models 22, 36, and 38, with occasionally predicted negative recruitment by the latter set to zero, compares favourable with the observed recruitment of the cod stock as derived from area-disaggregated MSVPAs ($r^2 = 0.72$) (Fig. 9*a*). Recruitment in 1979 was underestimated by the model and overestimated in 1984. Some smaller deviations occurred during the later part of the time series when the model predicted higher recruitment than observed. The corresponding multiplicative model showed considerably larger deviations in the beginning of the time series, consistently underestimating recruitment ($r^2 = 0.65$) (Fig. 9*b*). In the most recent years, deviations between observed and predicted recruitment were less than in the additive model.

Validation of stock–recruitment models

To test the sensitivity of the parameter estimates and the predictive power of the stock–recruitment relationships utilised to estimate recruitment in combined areas, model parameters were refitted excluding the first and last 4–5 years of data, respectively. For Subdivision 25, all data series revealed highly significant multiple linear regressions (Table 4). The explained variance was lowest when excluding the data for 1976–1980, *i*.e., time periods with high recruitment. Furthermore, the variable oxygen content in the reproductive volume was not significant in this model, while it was in all other scenarios. For Subdivision 26, the overall fit of the model was better than in the original version when excluding data from 1976 to 1979 and from 1976 to 1980, explaining 69 and 85% of the variance, respectively (Table 4). In contrast, runs excluding the most recent years resulted in a reduction of the explained variance (47–49%). In Subdivision 28, the explained variance was lowest when fitting the model to the period 1981–1995, while omitting the most recent data from the parameter estimation had a limited impact only.

Comparing the observed and predicted recruitment at age 0 summed over Subdivisions 25, 26, and 28 revealed a similar fit, independent of whether the last 4 or 5 years of data were used in the parameter estimation or not (Figs. 10*a* and 10*b*). Thus, the models were able to predict the increase in recruitment observed in 1993–1995. The models overestimated the recruitment in these years by 53–89%, while recruitment in 1992 was underestimated by 61–63%. However, this corresponds to the behaviour of the original model.

Excluding data from 1976–1979 revealed, in general, a good fit to the observed recruitment in the combined stock (Fig. 10*c*), with the recruitment in 1976 and 1980 being slightly more underestimated than by the original model version. Deviations in 1979, however, were rather pronounced,

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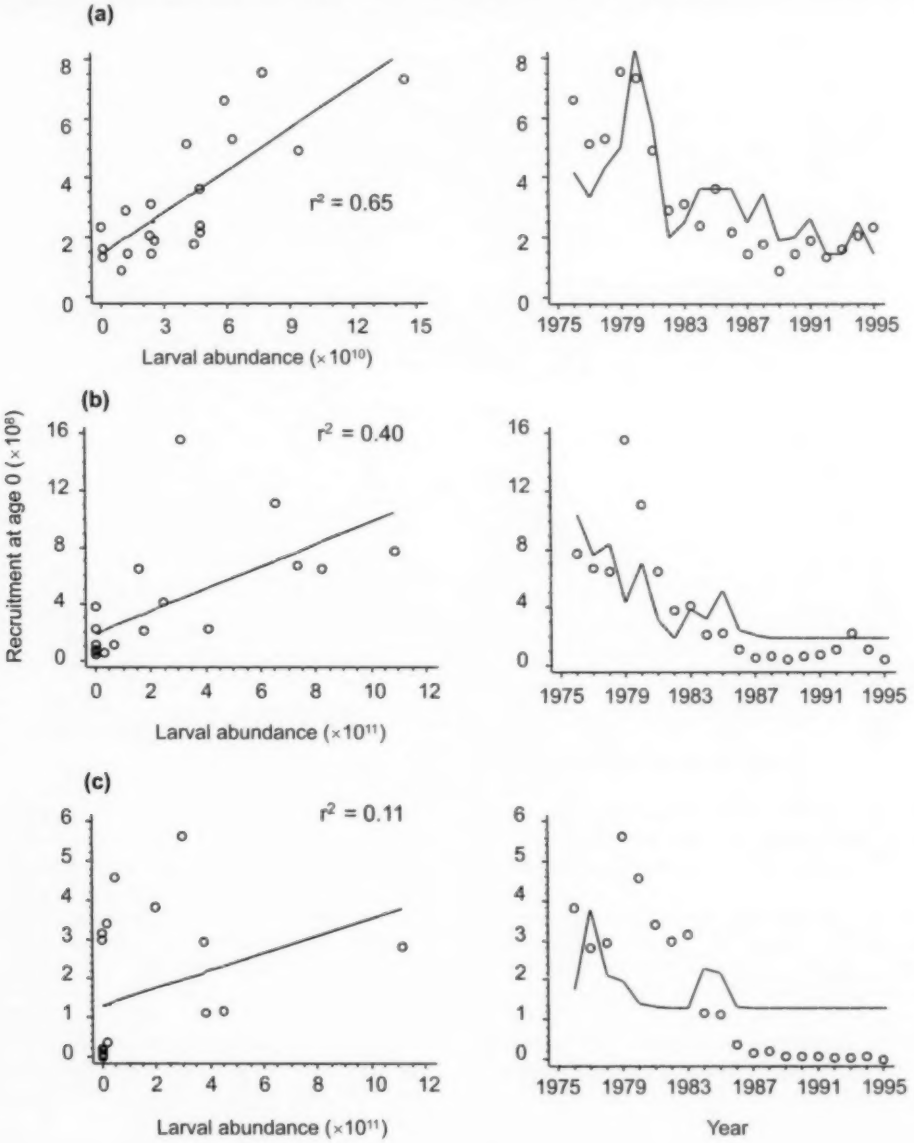
Fig. 3. Linear regressions of cod recruitment at age 0 on larval abundance in (*a*) Subdivision 25 (see model 15), (*b*) Subdivision 26 (see model 32), and (*c*) Subdivision 28 (see model 33). Circles, observed values; lines, predicted values.



with the observed value well outside the 95% prediction limit of the mean. This deviation is not caused by a single outlying event in a specific subdivision but is a general trend for all areas, being most pronounced in Subdivisions 25 and 26. Contrary to the reasonable behaviour of the models in the first three cases, starting the parameter estimation procedure in 1981 produced large deviations between observed and predicted recruitment in 1976–1980 (Fig. 10*d*). The model always substantially underestimated recruitment for these years and had considerably broader 95% prediction limits of the mean, with observed values being outside these limits in 1976, 1979, and 1980.

The predicted and observed recruitment at age 1 in the Central Baltic (Fig. 11*a*) showed somewhat higher deviations than recruitment at age 0, but still, an overall rather good agreement is evident (r^2 = 0.65). As a test, predicted recruitment at age 1 was compared with observed recruitment indices obtained by bottom trawl surveys. In general, the comparison revealed similar trends with declining recruitment throughout the first half of the 1980s and increasing recruitment in the 1990s (Fig. 11*b*). However, considerable deviations are apparent for some years, indicated also by the relatively low r^2 of 0.40. Predicted recruitment declined earlier, i.e., from 1981 onwards, compared with 1983 in the trawl survey but reached lowest levels not before 1989, while the trawl survey indicated low recruit-

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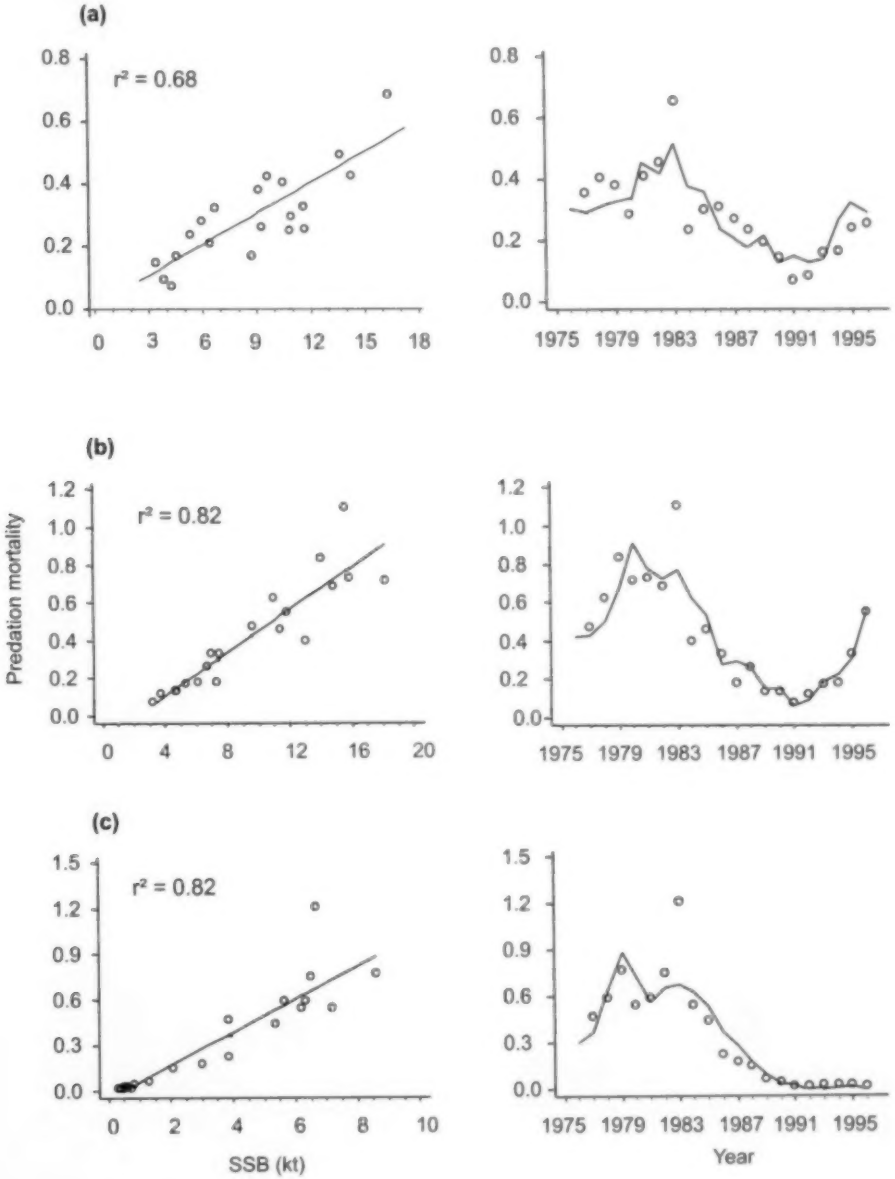
Fig. 4. Linear regressions of predation mortality coefficients of cod age-group 0 (second half of the year) on cod SSB in (*a*) Subdivision 25 (see model 20), (*b*) Subdivision 26 (see model 34), and (*c*) Subdivision 28 (see model 35). Circles, observed values; lines, predicted values.



ment already in 1985. In contrast, the increase in recruitment was already apparent in the trawl survey in 1991, while the predicted recruitment did not increase before 1993.

Discussion

Application of process-oriented recruitment modelling approaches including the results of detailed investigations of egg production, egg, larval, and juvenile survival, as well as oceanographic conditions has seldom been employed to examine variations in recruitment success of marine fish populations. Notable exceptions in the marine environment include plaice in the North Sea and the Irish Sea (e.g., Beverton and Iles 1992), walleye pollock in the North Pacific (e.g., Megrey et al. 1996), and anchovy in the Benguela Current (e.g., Painting et al. 1998). In these aforementioned cases, attempts are still ongoing, as indeed they are in the Baltic, with the major problem in all systems being the lack of availability of time series of key processes and the variety and complexity of processes involved.

Investigation of the link between environmental factors, spawning stock features, and reproductive success of Baltic

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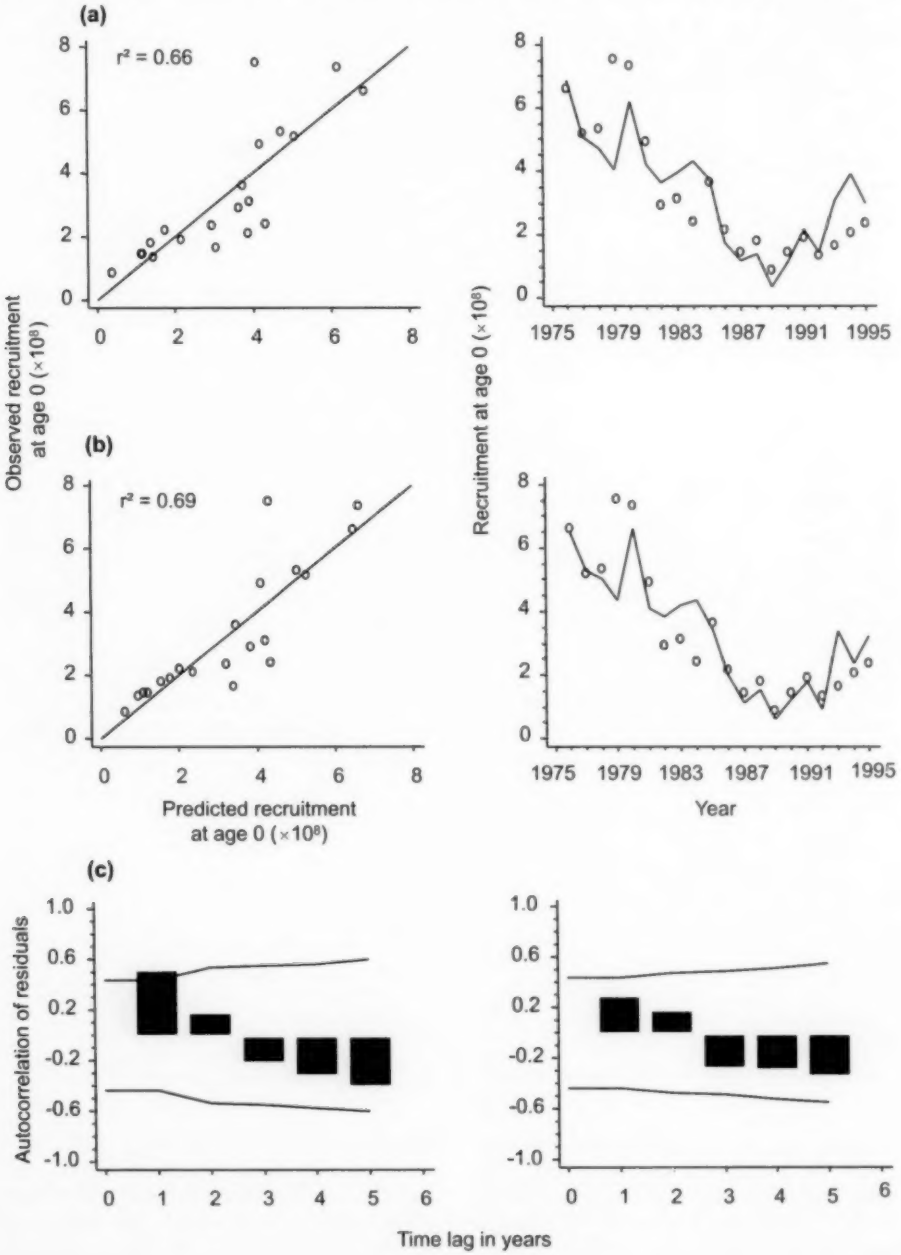
Fig. 5. Multiple linear regressions of cod recruitment at age 0 in Subdivision 25 on potential egg production corrected for egg consumption and oxygen content in the reproductive volume (see model 21). (*a*) Observed versus predicted recruitment; (*b*) same statistical model including the larval transport index as a further independent variable (see model 22); (*c*) autocorrelation of residuals of the first (left) and second model (right) including the 95% confidence limits. Circles, observed values; lines, predicted values.



cod has previously been performed by several investigators (e.g., Plikshs et al. 1993; Sparholt 1996; Jarre-Teichmann et al. 2000). A number of differences between these approaches and the present analysis exist. First, variables and processes considered in our exploratory analysis were based on extensive field, laboratory, and modelling activities, with their impact on specific early life stages well justified and not only detected via statistical analysis. Based on these activities, the key variables and approaches utilised included (*i*) disaggregation of recruitment success and spawning stock sizes into major spawning areas having distinct hydrographic regimes (MacKenzie et al. 2000) and exhibiting dif-

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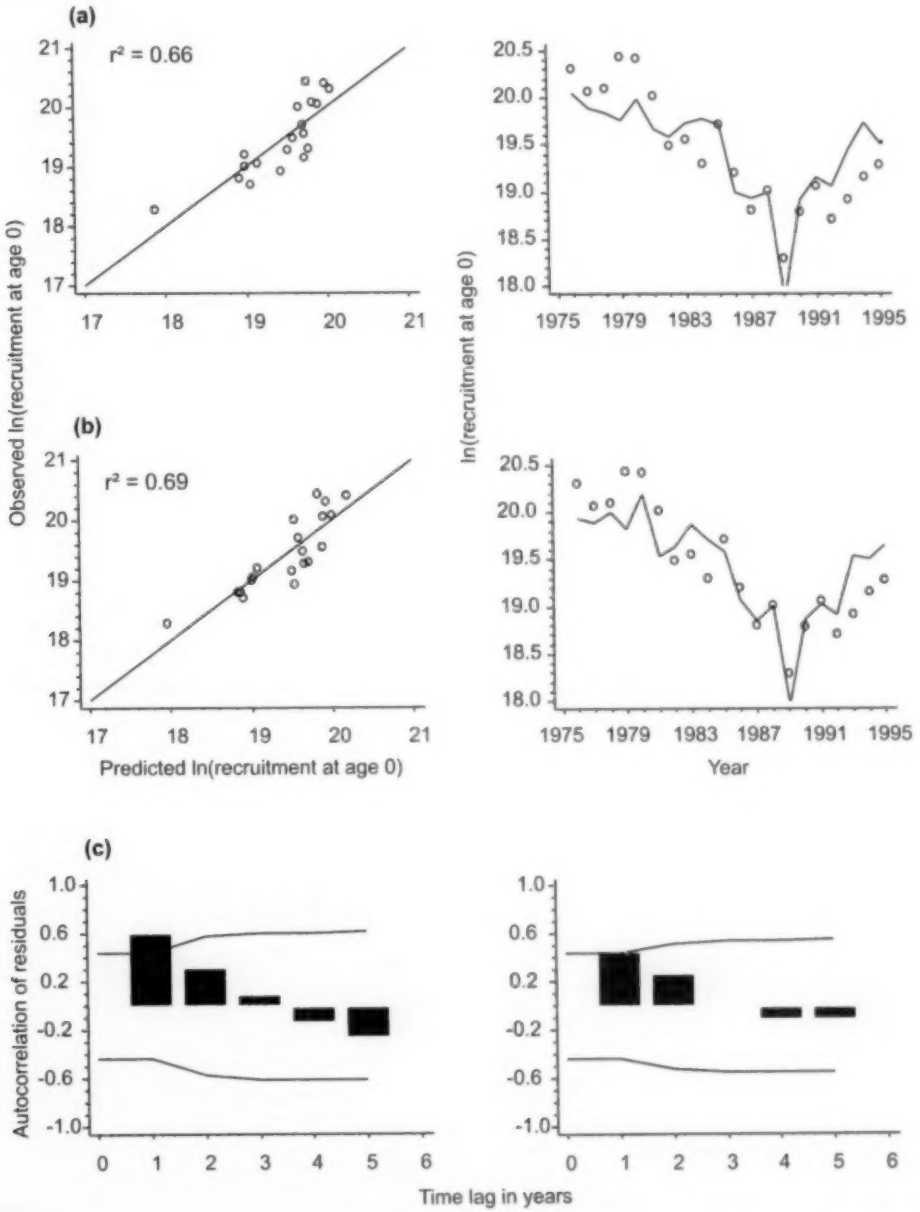
Fig. 6. Multiple linear regressions of ln-transformed cod recruitment at age 0 in Subdivision 25 on ln-transformed potential egg production corrected for egg consumption and oxygen content in the reproductive volume (see model 24) (*a*) Observed versus predicted recruitment; (*b*) same statistical model including the ln-transformed larval transport index as a further independent variable (see model 25); (*c*) autocorrelation of residuals of the first (left) and second model (right) including the 95% confidence limits. Circles, observed values; lines, predicted values.



ferences in the individual maturation process (Tomkiewicz et al. 1997), recruitment success, and stock development trends (Sparholt and Tomkiewicz 2000; Köster et al. 2001), (*ii*) utilisation of the potential egg production as a measure of reproductive effort by applying time series of sex-specific maturity ogives (Tomkiewicz et al. 1997) and relative fecundity values exhibiting significant interannual variability (Kraus et al. 2000), (*iii*) quantifying the impact of suboptimal but not lethal oxygen concentrations (Rohlf 1999) in the reproductive volume of the Bornholm Basin, the only spawning area typically characterised by conditions suitable for cod egg development (MacKenzie et al. 2000), (*iv*) incorporation of cod egg predation by clupeids (Köster and Möllmann 2000*a*), and (*v*) testing the effect of a cumulative wind energy

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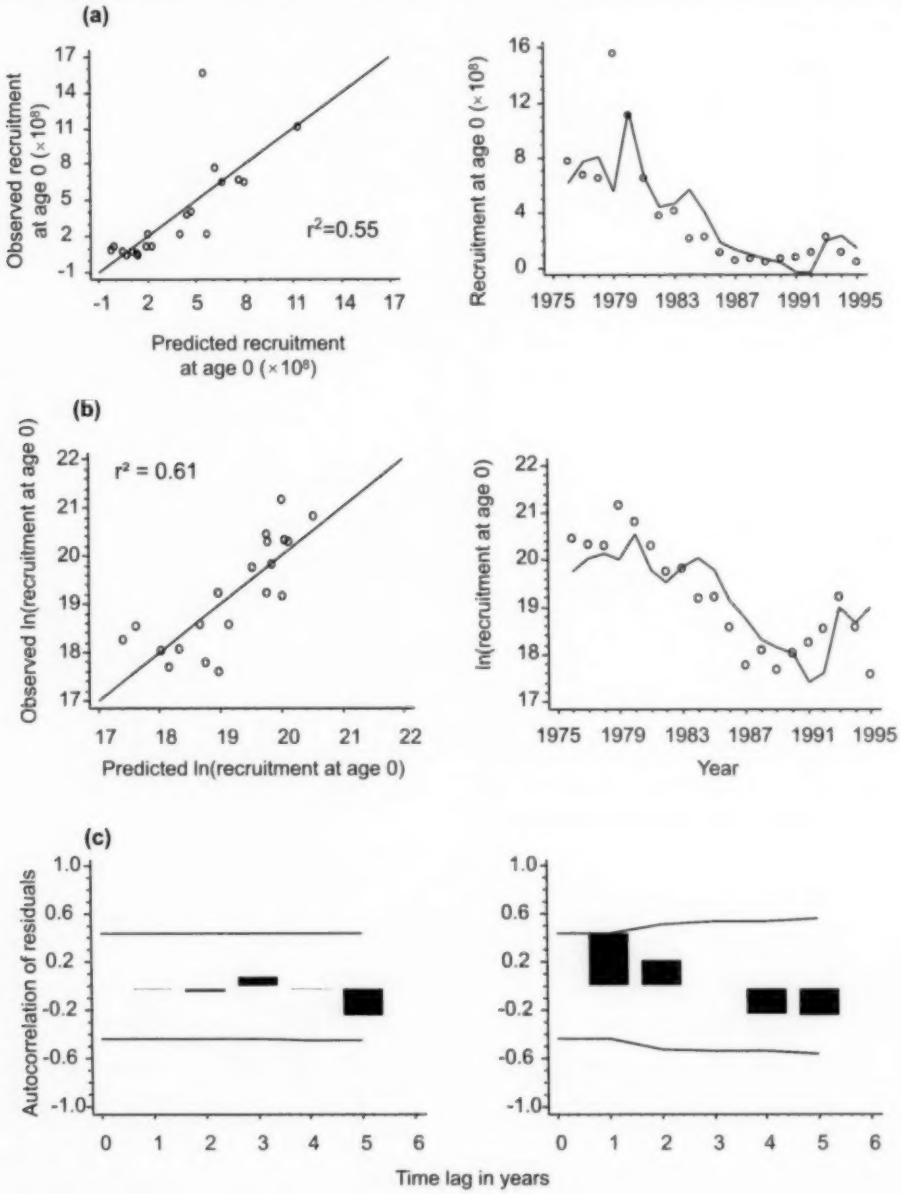
Fig. 7. Multiple linear regressions of cod (*a*) observed versus predicted recruitment at age 0 in Subdivision 26 on potential egg production and reproductive volume (see model 36); (*b*) same variables with ln-transformed data (see model 40); (*c*) autocorrelation of residuals of the first (left) and second model (right) including the 95% confidence limits. Circles, observed values; line, predicted values.



index as a measure of larval retention in spawning basins or transport to nursery areas (Voss et al. 1999; Hinrichsen et al. 2001).

Explanation of variability in stock–recruitment relationships

Survival during the egg stage

The present analysis assumes that potential egg production based on the spawning stock characteristics is an unbiased measure of the actual egg production in the field, an assumption justified by a significant relationship between daily production of egg stage IA during main spawning time obtained from ichthyoplankton surveys in Subdivision 25 and the estimated potential production by the SSB in 1986–1996. Thus, it appears to be unlikely that encountered deviations between observed and predicted egg survival rates can be explained by grossly erroneous egg production estimates.

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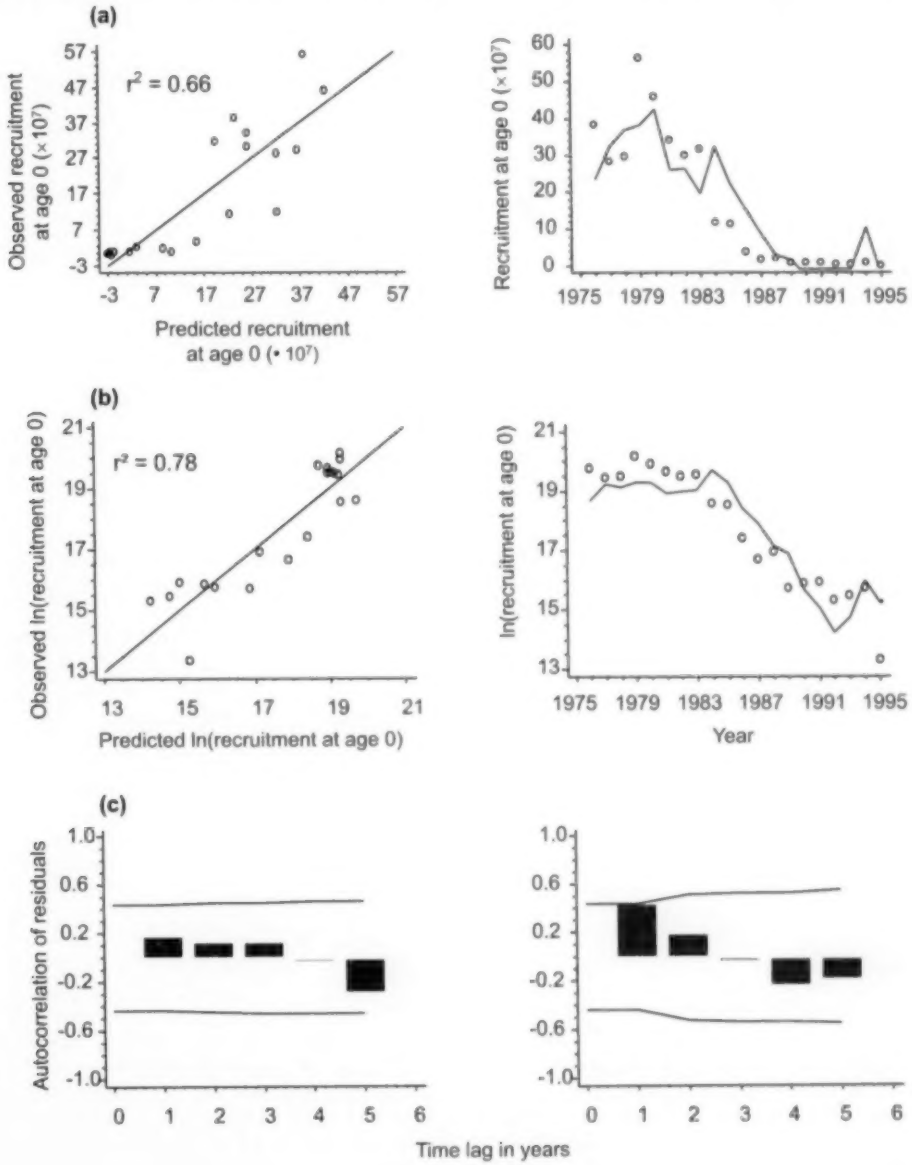
Fig. 8. Multiple linear regressions of cod (*a*) observed versus predicted recruitment at age 0 in Subdivision 28 on potential egg production and reproductive volume (see model 38); (*b*) same variables with ln-transformed data (see model 41); (*c*) autocorrelation of residuals of the first (left) and second model (right) including the 95% confidence limits. Circles, observed values; line, predicted values.



However, a remarkable deviation between potential and realised egg production was encountered in 1996, with the former estimate being considerably higher than the latter.

The performed exploratory analysis revealed a significant impact of oxygen and predation on egg survival until developmental stage III in Subdivision 25. It should be noted that an "observed" high egg survival in 1994 and relatively low survival in 1995 and 1996 were not consistent with the statistical model developed. The hydrographic regime in 1994 was characterised by higher than average salinities and, in the beginning of the spawning season, high oxygen concentrations in and below the halocline. However, as the spawning peak was late in the year, eggs were nevertheless exposed to relatively low oxygen levels (MacKenzie et al. 1996), thereby resulting in oxygen-related survival rates similar to those in 1995 and 1996 (54–60%). Egg predation by sprat was lower from 1993 on than in preceding years and was caused by (*i*) a continuous shift in spawning time of cod to a later month (Wieland et al. 2000), resulting in a limited temporal overlap between sprat as predators and cod eggs as prey (Köster and Möllmann 2000*a*) and (*ii*) a limited vertical overlap between predator and prey due to the

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Fig. 9. Observed and predicted cod recruitment at age 0 in combined Subdivisions 25, 26, and 28 based on potential egg production including environmental factors incorporated into (*a*) additive models 22, 36, and 38 and (*b*) multiplicative models 25, 40, and 41. Open circles, observed values; solid circles, predicted values.

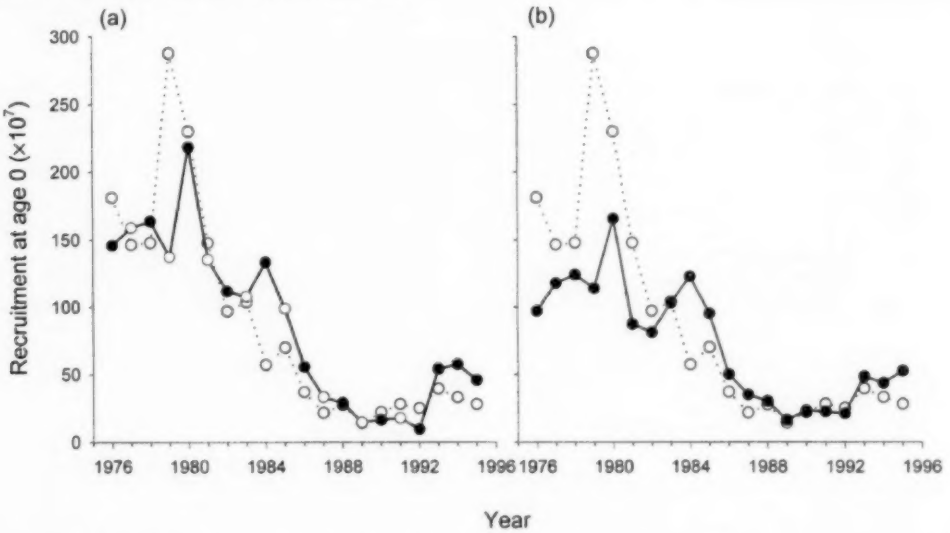

Table 4. Coefficients of determination and significance levels of parameters of multiple linear regressions relating recruitment at age 0 in different subdivisions with potential egg production and environmental variables (model configurations 22, 36, and 38) utilising different data subsets of the time series for estimation of the parameter values.

Subdivision		1976–1995	1980–1995	1981–1995	1976–1990	1976–1991
25	r^2 value (adjusted)	0.69	0.69	0.57	0.69	0.71
	Intercept	0.452	0.400	0.023	0.337	0.271
	Potential egg production – egg predation	<0.001	<0.001	<0.001	0.008	0.003
	Oxygen content in reproductive volume	0.012	0.012	0.655	0.020	0.015
	Larval transport index	0.118	0.189	0.450	0.330	0.237
26	r^2 value (adjusted)	0.55	0.85	0.69	0.47	0.49
	Intercept	0.523	0.115	0.608	0.657	0.722
	Potential egg production	0.005	<0.001	<0.001	0.048	0.037
	Reproductive volume	0.032	0.002	0.234	0.064	0.055
28	r^2 value (adjusted)	0.66	0.69	0.56	0.61	0.58
	Intercept	0.383	0.518	0.710	0.431	0.393
	Potential egg production	<0.001	<0.001	<0.001	<0.001	<0.001
	Reproductive volume	0.088	0.961	0.952	0.058	0.063

changed hydrographic regime (Köster and Möllmann 2000*a*). This decrease in predation pressure was partly offset by an increase in consumption by herring in summer. Thus, observed differences in egg survival rates between 1993–1994 and subsequent years are not explainable by the considered environmental processes. A validation of the MSVPA results based on independent population estimates revealed an overestimation of the cod spawning population in Subdivision 25 in 1996 (Köster et al. 2001). Consequently, the potential egg production is an overestimation as well, which in turn leads to an underestimation of the observed egg survival rates, hence, partly explaining the discrepancy.

Survival until the larval stage

The exploratory analysis was unable to explain a considerable part of the variability encountered between different egg production measures and larval abundance in Subdivision 25. This indicates either that (*i*) factors other than oxygen- and predation-related mortality influence the survival until the larval stage, (*ii*) the variability in larval abundance (integrated over all developmental stages) is too high to detect a major impact of both mentioned factors, or (*iii*) the abundance estimates of larvae may be too variable due to inadequate spatial and temporal sampling strategies.

Behaviour studies conducted with larvae demonstrated that low oxygen concentration has an impact on larval mortality (Nissling 1994) and that egg incubation at low oxygen concentration impacts on larval activity as well (Rohlf 1999). Furthermore, the experiments revealed that vertical migration into upper water layers is not started before day 4 after hatch. Hence, a significant impact of the environment within and below the halocline on larval survival can be expected. Due to differences in buoyancy and minimum lethal oxygen concentrations in the egg and larval stage (Rohlf 1999), it appears to be unlikely that the oxygen-related egg survival is a suitable measure of oxygen-related survival

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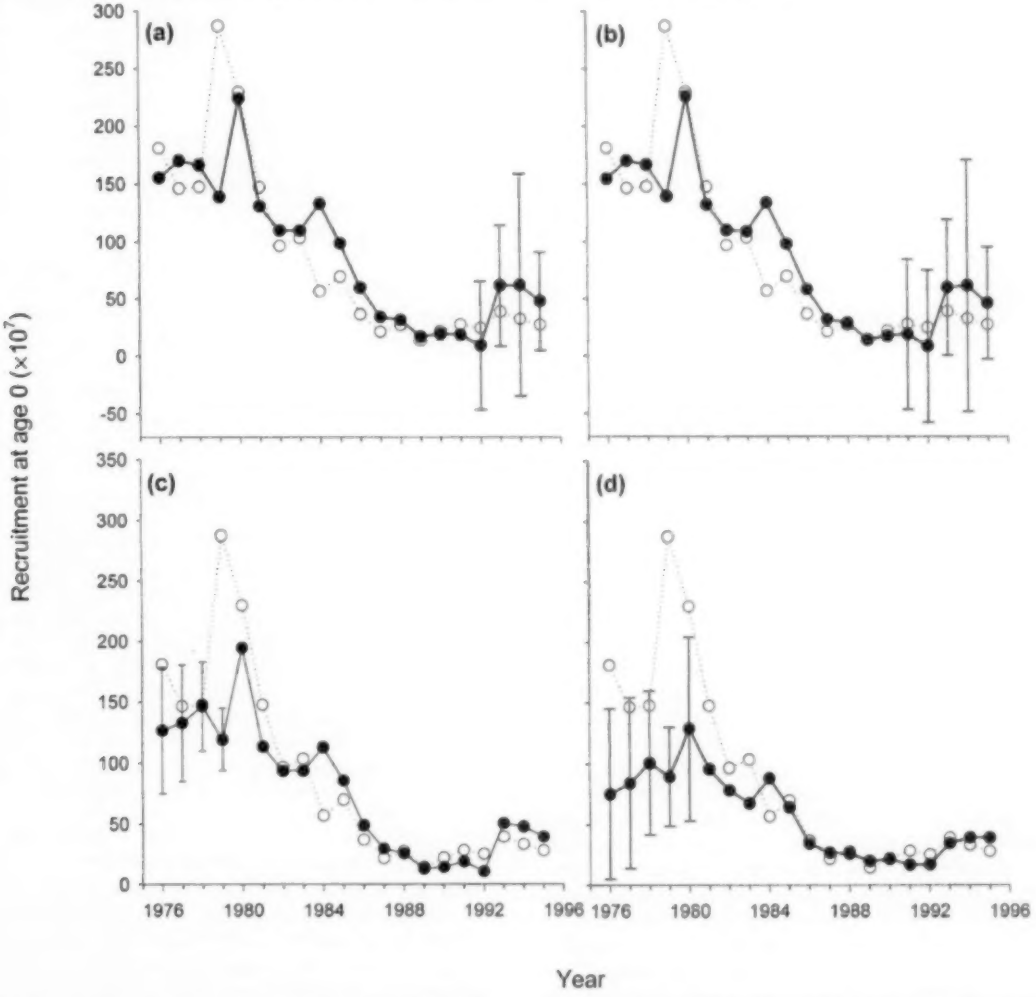
Fig. 10. Observed and predicted cod recruitment at age 0 in combined Subdivisions 25, 26, and 38 based on potential egg production including environmental factors (models 22, 36, and 28) utilising different subsets of data for parameter estimation: (*a*) 1976–1991, (*b*) 1976–1990, (*c*) 1980–1995, and (*d*) 1981–1995. Shown are the 95% confidence limits of the predicted means for recruitment in years excluded from fitting the model. Open circles, observed values; solid circles, predicted values.



probability of larvae. In fact, the oxygen content in the reproduction volume performed better in the exploratory analysis and hence was also included in the more complex model configurations for Subdivision 25.

A multiple linear regression of larval abundance and potential egg production corrected for egg predation and the oxygen content in the reproductive volume exhibited large negative residuals in recent years. This suggests a mismatch in the timing of the plankton surveys and time periods of high larval abundance caused by a delayed spawning (Wieland et al. 2000) in these years. This of course has implications for the use of the larval abundance estimates as a potential predictor of recruitment.

In the more eastern spawning areas, variability in larval abundance was more easily explained, as a highly significant impact of the hydrography is obvious. This result is not surprising, as the environmental conditions are less favourable for successful egg survival in these areas compared with the Bornholm Basin (MacKenzie et al. 2000). However, a high reproductive volume does not necessarily result in high survival of early life stages. In 1994, an extremely high reproductive volume was encountered in the Gotland Basin due to an inflow into this basin. This inflow displaced the anoxic bottom water upwards (CORE 1998), resulting in an intermediate layer with insufficient oxygen concentration but densities sufficient to keep cod eggs floating, hence creating conditions detrimental to the development of cod eggs. Situations like these clearly demonstrate the potential for index improvement through the development of models for predicting the vertical distribution of cod eggs in all spawning areas relative to oxygen conditions.

Survival from the larval to the 0-group stage

The significant linear relationship between larval abundance and recruitment at age 0 in Subdivision 25 was not enhanced by inclusion of any additional variable, e.g., the

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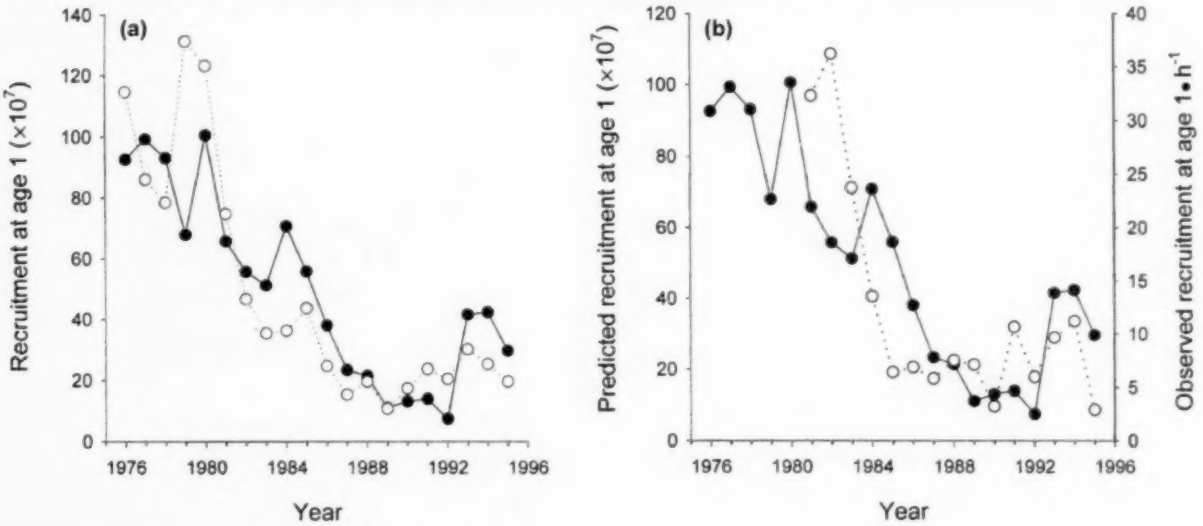
Fig. 11. Observed and predicted cod recruitment at age 1 in combined Subdivisions 25, 26, and 28 based on predicted 0-group recruitment from additive models 22, 36, and 38 and applied predicted 0-group predation mortalities (solid circles). Observed recruitment (open circles) as derived by (*a*) area-disaggregated MSVPA and (*b*) catch rates obtained from the international bottom trawl survey.



oxygen content in the reproductive volume or the larval transport index. This identifies the applicability of the simple model for predicting recruitment. In Subdivision 26, a significant relationship between larval abundance and recruitment was also obtained, but the fit of the model was less satisfactory, while for Subdivision 28, no significant relationship could be established. This can be explained by the fact that recruitment success occurred in this area despite the lack of larvae in the ichthyoplankton. As recruitment was not only determined by the MSVPA but also observed in the bottom trawl surveys as age-group 1, this indicates either (*i*) a problem in sampling efficiency of larvae at low larval abundance or (*ii*) a transport of larvae and the pelagic 0-group out of the Bornholm area into the more eastern Baltic basins. The latter hypothesis is supported by hydrodynamic modelling (Hinrichsen et al. 2001) and comparison of trawl survey results and MSVPA output (Köster et al. 2001) and is also indicated by the fact that the parameter estimate for the larval transport index is negative in Subdivision 25.

Survival during the 0-group stage

The linear relationship between MSVPA-derived cannibalism rates and cod SSB may to a certain extent be artificially created by the estimation procedure implemented in the MSVPA. Here, the predation mortalities depend to a considerable degree on the predator stock size, if consumption rates and suitability coefficients are kept constant over time (Neuenfeldt and Köster 2000). In MSVPA runs used for the present analysis, suitability coefficients averaged over years are still in use. This impacts on not only predation mortalities but also recruitment values utilised in our analysis. Neuenfeldt and Köster (2000) compared recruitment estimates derived by MSVPA with and without a suitability submodel, i.e., utilising available yearly stomach content data for estimation of the predation mortalities. According to this test, the impact on the derived Central Baltic cod recruitment is, in general, limited, i.e., the estimates are highly correlated (r^2 = 0.84). However, the estimated strengths of the 1979 and 1980 year-classes are considerably overestimated by the MSVPA with a suitability submodel compared with the direct estimates (Neuenfeldt and Köster 2000), while the 1977 year-class strength is underestimated. As application of the MSVPA without a suitability submodel is restricted to years with sufficient stomach content data, this procedure is at present no alternative to the standard MSVPA. However, it indicates that a revision of the suitability submodel implemented in the MSVPA is needed to determine recruitment as reliably as possible.

Validation of stock–recruitment models

The models established for the eastern spawning areas are simpler than those established for the Bornholm Basin. In the latter area, a water volume suitable for successful development of eggs, the so-called reproductive volume, was always available (Plikshs et al. 1993; MacKenzie et al. 2000). Other factors such as egg predation (Köster and Möllmann 2000*a*) have a regular and also more pronounced influence on the reproductive success of cod in this basin. In the Gdansk Deep and especially in the Gotland Basin, the hydrographic regime did not, in general, allow successful egg development (MacKenzie et al. 2000). Hence, relatively simple models, incorporating the potential egg production and the reproductive volume as variables, were required for these areas to achieve a reasonable explanation of recruitment variability.

The statistical models 22 and 25 established for Subdivision 25 contain a larval transport index with a negative regression coefficient, i.e., recruitment success appears to be negatively related to high wind stress, suggesting that retention in the basin and low turbulent mixing lead to increased recruitment success, contradicting the hypothesis that a rapid transport into nursery areas is a process enhancing recruitment success (Jarre-Teichmann et al. 2000; Hinrichsen et al.

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2001). However, this result is biologically sensible when interpreted as a transport into neighbouring Subdivisions 26 and 28, for which evidence exists (Köster et al. 2001). Jarre-Teichmann et al. (2000) demonstrated that wind energy is positively related to recruitment success at age 2 in Baltic cod, assuming the wind forcing in the Bornholm Basin to be representative of the entire Central Baltic. Thus, wind-induced advective gains and losses between different subdivisions are not resolved in their analysis. For detection of the impact of transport to coastal nursery areas on recruitment, this approach is of advantage, compared with ours in which rapid transport will result also in loss of specimens to neighbouring subdivisions. Inclusion of the larval transport index developed for Subdivision 25 in recruitment model 36 revealed a positive impact of the transport index on recruitment in Subdivision 26, but not being significant. Resolving advective processes between different areas more adequately is in principal possible, but requires further hydrodynamic modelling under various area-specific environmental forcing scenarios for development of enhanced larval transport indices.

To obtain an indication of the sensitivity of the parameter estimates and the predictive power, models 22, 36, and 38 were refitted over different shorter time periods and model predictions then compared with the excluded year's observations. The exercise clearly demonstrated that the models derived for the different subdivisions are not sensitive to the exclusion of periods from the parameter estimation procedure. The models were able to capture the trend of high recruitment during the late 1970s and early 1980s relatively well and the low recruitment in the early 1990s very well. However, if all observed high recruitment values were excluded from the time series utilised for parameter estimation, a substantial underestimation of recruitment in early years was obvious.

Recruitment was lognormally rather than normally distributed. Thus, multiplicative instead of additive processes may be more appropriate in some of the models (Sparholt 1996). Additionally, established multiplicative models explained more of the variance in recruitment in Subdivisions 26 and 28. However, the ln-transformed model did not exhibit better predictive power and consistently underestimated recruitment at high reproductive success in the beginning of the time series in all areas. Additionally first-order correlations in residuals were encountered regularly in all multiplicative models, whereas this was less pronounced in the additive models. Other measures about which model type to prefer were more inconclusive, e.g., normality of residuals, heteroscedasticity, and correlation of variables, with no model behaving considerably better. A possible correction of the multiplicative model for time series bias (Hilborn and Walters 1992) may, however, enhance its predictive performance.

Independent of the model choice, an underestimation of the recruitment was encountered for 1979 in all subdivisions. Although the potential egg production was lower than in preceding and subsequent years and the reproductive volume was well below average in all basins, recruitment at age 0 as determined by the MSVPA was highest. Sparholt (1996) described similar deviations between observed and predicted recruitment of the 1979 year-class when applying a multiplicative model for the Central Baltic incorporating cod SSB, the reproductive volume, and the SSB of sprat as independent variables and recruitment estimated by MSVPA as the dependent variable. As unfavourable hydrographic conditions were measured throughout 1979 in all basins (MacKenzie at al. 2000), egg and larval abundances, especially in the eastern areas, were intermediate (Plikshs et al. 1993), and 1-group abundance indices from trawl surveys were above average but not extraordinary high (ICES Baltic trawl survey database), it appears to be likely that the "observed" recruitment derived by the MSVPA caused the deviations. This is confirmed by a significantly lower recruitment of the 1979 year-class at age 1 derived by a MSVPA run without a suitability submodel (Neuenfeldt and Köster 2000) compared with the standard MSVPA. Excluding the 1979 data from the model fitting increased the explained variance in 0-group recruitment in Subdivisions 25 and 26 substantially to 80 and 87%, respectively.

Another bias affecting the estimation of cod recruitment by the MSVPA is misreporting, identified to have occurred especially in 1992–1994 (Köster et al. 2001). Underestimated catch at age most likely resulted in underestimated strengths of the 1990–1992 year-classes, partly explaining deviations between predicted and observed recruitment from the international bottom trawl survey.

Applicability of stock–recruitment models

The stock–recruitment models established here explain a considerable part of the variability encountered in cod recruitment in the Baltic Sea. The remaining variability may be due to a number of processes not included in the present exercise such as egg fertilisation (Vallin et al. 1999) and the influence of parental characteristics (age and size structure, condition) on egg and larval characteristics (buoyancy, survival probability, e.g., Marshall et al. 1998; Trippel 1998) and a potential starvation of larvae due to a shortage of suitable food supply (Grønkjær and Wieland 1997) but also uncertainties in the way that variables are assumed to represent processes of interest (e.g., reproductive volume effect on egg survival, predation relative to predator–prey overlap). Results from recent studies on these topics are becoming available for Baltic cod (e.g., Nissling et al. 1998) and potentially could also be incorporated into new generations of recruitment models (Vallin et al. 1999). Apart from these potential improvements, major difficulties in establishing environmentally sensitive stock–recruitment models are to (*i*) incorporate various factors affecting different early life stages (Paulik 1973) in one model relating egg production by the spawning stock to subsequent recruitment, (*ii*) resolve the potential nonlinearity and additive effects of different factors on subsequent early life stages, and (*iii*) determine the historical recruitment at age 0 or 1 originated by specific spawning components. The first problem has been described in detail previously (Rothschild 1986; Ulltang 1996). Bailey et al. (1996) and Campana et al. (1989) considered it explicitly when constructing survival curves of walleye pollock as well as Nova Scotia cod and haddock cohorts relative to their physical and biological environment. For the Baltic, however, this type of approach has not been conducted (for a discussion of previous stock–recruitment models, see Jarre-Teichmann et al. 2000). The third difficulty involves estimating recruitment before juveniles recruit to the fishery and is as well described theoretically (Hilborn and Walters 1992)

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but is often neglected in recruitment modelling approaches (Ulltang 1996). In our analysis, problems in the estimation of recruitment are apparent when inspecting model residuals but also from discussions on the validity of the MSVPA approach to estimate recruitment, specifically for distinct areas (Köster et al. 2001).

Despite these shortcomings and uncertainties, the presented stock–recruitment models may be utilised for enhancing short-term recruitment predictions. The predictions could be based on (*i*) the most recent female SSB coupled to relative fecundity estimates, (*ii*) hydrographic conditions during spawning periods and at spawning sites, which would enable prediction of the egg and larval survival in relation to ambient oxygen concentrations, and (*iii*) cod egg predator population sizes as well as spatial overlap between predator and prey, both forced by hydrographic processes.

A number of potential improvements to the stock–recruitment models are possible through the better resolution of the influences of a number of key variables. Here, the most promising potential candidates are (*i*) including variations in buoyancy of eggs spawned by first-time and repeat spawners (Vallin et al. 1999), (*ii*) resolving the vertical distribution of cod eggs in relation to oxygen concentration in eastern spawning areas, and (*iii*) including the effects of hydrodynamic processes on the horizontal and vertical overlap of predator and prey including cannibalism also.

The spatially disaggregated approach presented here allows an investigation of the impact of different stock components on the reproductive success of cod in the Central Baltic. This is a necessary prerequisite for area-based fisheries management, i.e., an area closure within the Bornholm Basin during cod spawning time recommended by the International Baltic Sea Fisheries Commission (IBSFC 1999).

The stock–recruitment models developed here have the potential to be employed in medium- to long-term stock projections through the incorporation of simulated environmental variability and alternative exploitation scenarios. However, advances need to be made in a number of areas in order to improve these predictions. First, we would like to emphasise that processes coupling individual growth, sexual and gonadal maturation, as well as quantity and quality of produced spawning products to environmental conditions (e.g., Marshall and Frank 1999; Trippel 1998) are a promising field of research in this respect. Furthermore, anthropogenic impacts, such as contamination by toxic substances, potentially affecting the viability of spawning products and eutrophication and impacting the oxygen consumption rates in deep Baltic basins and thus the ambient oxygen conditions for cod egg development (e.g., MacKenzie et al. 1996) have to be verified and incorporated when projecting over longer time periods. Finally, the importance of structural uncertainty in medium- to long-term projection models, i.e., which variables to incorporate and how to incorporate them into the model (e.g., linear, exponential, additive), remains an area for further development; a key issue in the development of quantitative relationships between environmental variables and fish populations as interactions may be counterintuitive (Rose 2000).

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Appendix

Table A1. Potential seasonal cod egg production by the spawning stock, egg abundance, realised daily egg production at stages I and III during main spawning season, larval abundance from ichthyoplankton surveys, recruitment at age 0 from area-disaggregated MSVPA, reproductive volume, oxygen content within the reproductive volume (summed over 1-m depth intervals), oxygen-related proportions of egg survival, egg predation index, and larval transport index in Subdivision 25.

Year	Potential egg production (no. × 10^{12})	Egg abundance (no. × 10^{9})	Realised production egg stage I (no. × 10^{9})	Realised production egg stage III (no. × 10^{9})	Larval abundance (no. × 10^{9})	Recruits 0-group (no. × 10^{6})	Reproductive volume (km^3)	Oxygen content in reproductive volume ($m \cdot mL \cdot L^{-1}$)	Oxygen-related egg survival	Egg predation index	Larval transport index ($W \cdot m^{-2}$)
1976	44.25	936			59.25	661.6	251.2	215.3	0.90	0.004	138 076
1977	40.25	553			41.48	517.4	249.1	118.7	0.52	0.013	64 352
1978	48.94	691			62.81	532.9	128.7	73.9	0.74	0.040	12 821
1979	36.28	640			77.03	753.7	74.0	74.9	0.65	0.019	41 333
1980	42.80	1304			144.57	734.6	232.4	193.9	0.73	0.023	12 334
1981	54.41	249			94.80	493.6	62.5	27.6	0.20	0.058	92 364
1982	54.02	332			11.85	291.2	85.7	25.8	0.15	0.089	–8 203
1983	38.13	527			23.70	311.4	169.6	67.6	0.66	0.035	22 794
1984	50.02	486			47.39	240.3	120.2	69.0	0.64	0.068	84 371
1985	33.82	593			47.43	363.2	132.4	84.8	0.58	0.046	120 216
1986	23.75	658	11.39	1.60	46.99	218.4	98.5	84.3	0.23	0.226	45 903
1987	18.02	326	17.10	2.05	23.70	145.6	94.9	33.1	0.30	0.184	92 628
1988	15.99	172	14.66	1.66	43.93	180.0	99.9	48.9	0.08	0.173	–29 700
1989	16.03	178	13.42	1.83	9.66	87.5	70.7	9.4	0.12	0.267	31 016
1990	11.94	154	12.30	0.84	12.56	145.3	80.3	29.7	0.21	0.131	72 811
1991	8.30	201	18.80	1.74	25.24	189.3	184.7	105.5	0.50	0.069	132 791
1992	12.30	107	17.37	0.85	0.71	134.0	161.3	45.7	0.18	0.113	133 864
1993	13.24	395	16.54	2.43	0.59	164.5	207.7	137.8	0.61	0.039	–14 550
1994	36.96	1970	91.95	10.66	23.26	208.3	194.7	71.9	0.59	0.037	196 622
1995	36.86	1749	108.08	3.70	0.09	235.1	92.0	31.8	0.60	0.068	13 040
1996	34.53	602	50.18	3.83	5.24	661.6	126.0	43.2	0.54	0.057	

Table A2. Potential seasonal cod egg production by the spawning stock, egg abundance during main spawning season, larval abundance from ichthyoplankton surveys, recruitment at age 0 from area-disaggregated MSVPA, and reproductive volume in Subdivisions 26 and 28.

	Subdivision 26					Subdivision 28				
Year	Potential egg production (no. × 10^{12})	Egg abundance (no. × 10^{9})	Larval abundance (no. × 10^{9})	Recruits 0-group (no. × 10^{6})	Reproductive volume (km^3)	Potential egg production (no. × 10^{12})	Egg abundance (no. × 10^{9})	Larval abundance (no. × 10^{9})	Recruits 0-group (no. × 10^{6})	Reproductive volume (km^3)
1976	27.57	1163	108.59	768.0	142.3	15.89	240	57.60	382.3	141.0
1977	39.52	804	72.99	667.3	151.9	24.33	1334	320.64	280.6	174.9
1978	43.74	804	82.00	652.0	145.3	45.90	998	108.48	293.8	0
1979	46.01	27	31.09	1560.6	48.1	52.34	504	86.40	562.0	0
1980	72.68	518	65.33	1109.0	153.6	52.27	154	14.40	457.3	0
1981	68.09	355	15.77	645.0	1.1	39.52	1176	4.80	338.9	0
1982	48.20	9	0	378.1	1.1	39.81	119	0.00	298.8	0
1983	36.38	176	24.78	410.7	54.7	27.17	536	0.00	314.4	8.17
1984	53.25	121	17.12	210.8	23.8	43.81	230	129.60	119.3	23.00
1985	38.03	27	40.55	220.9	26.0	32.53	310	110.40	114.5	15.07
1986	23.51	20	6.76	114.8	4.7	24.89	61	4.80	36.6	0
1987	18.87	88	2.70	53.1	0.9	16.18	10	0	17.4	0
1988	16.62	0	0	71.2	0	8.63	0	0	22.6	0
1989	13.42	10	0	47.9	0	6.91	10	0	6.7	0
1990	11.51	34	0	67.6	0	2.54	26	0	7.8	0
1991	5.22	0	0	83.4	0	1.46	0	0	8.1	0
1992	6.77	29	0	111.8	0	0.74	11	0	4.4	0
1993	11.05	9	0	223.8	53.0	1.16	0	0	5.1	0
1994	13.18	116	0	115.4	81.0	1.55	38	0	6.8	175.0
1995	22.92	39	0	43.4	21.1	2.00	9	0	0.6	0
1996	34.44	22	0	768.0	20.5	1.51	17	0	382.3	0

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Characterizing fish populations: effects of sample size and population structure on the precision of demographic parameter estimates

J.P. Kritzer, C.R. Davies, and B.D. Mapstone

Abstract: We examined precision of size, age, growth, and mortality parameters for four reef fishes at sample sizes ranging from 25 to 1000 using bootstrapped population samples. The results are illustrative rather than prescriptive in that we do not determine "optimum" sample sizes, but rather describe improvements in precision with increasing sample size. Furthermore, we do not address the related issue of accuracy. In general, a sample size needed to be tripled to halve precision at that sample size. Mean lengths and ages were most precise, reaching 10% by a sample size of 75 for all species. von Bertalanffy growth parameters were up to an order of magnitude more precise when constraints were placed upon the fitting process. Asymptotic lengths, L_∞, were up to eight times as precise as Brody growth coefficients, K. Catch curves were generally less precise than two other mortality estimators, but we cannot advocate any estimator until accuracy is addressed. We propose a general rule of collecting an average of 7–10 fish per age-class to estimate a variety of parameters. However, we more strongly suggest applying similar analyses for focal species and, where possible, with consideration of the application of parameters (e.g., sensitivity analyses).

Résumé : À l'aide d'échantillons de populations soumis au bootstrap, nous avons examiné la précision des paramètres de taille, d'âge, de croissance et de mortalité pour des échantillons de 25 à 1 000 individus chez quatre poissons de récifs. Nos résultats sont illustratifs plutôt que prescriptifs parce que nous n'avons pas déterminé la taille « optimale » des échantillons, mais plutôt décrit l'amélioration de la précision avec la taille croissante de l'échantillon. Nous n'avons pas non plus considéré le problème apparenté de l'exactitude. En général, il faut tripler la taille de l'échantillon pour réduire de moitié la précision à cette taille d'échantillon. Les longueurs moyennes et les âges sont les variables les plus précises, atteignant 10% pour une taille d'échantillon de 75 chez toutes les espèces. Les paramètres de croissance de von Bertalanffy sont plus précis par un facteur allant jusqu'à 10 lorsque des contraintes sont placées sur le processus d'ajustement. Les longueurs asymptotiques, L_∞, sont jusqu'à huit fois plus précises que les coefficients de croissance de Brody, K. Les courbes de capture sont généralement moins précises que deux autres estimateurs de la mortalité, mais nous ne pouvons en recommander aucun tant que la question de l'exactitude n'aura pas été étudiée. Nous proposons, comme règle générale, de récolter en moyenne sept à 10 poissons par classe d'âge pour l'estimation d'une variété de paramètres. Cependant, nous suggérons encore plus fortement de faire subir des analyses semblables aux espèces-cibles et, quand c'est possible, de tenir compte de l'application des paramètres (e.g., des analyses de sensibilité).

[Traduit par la Rédaction]

Introduction

The precision and accuracy of a parameter estimate for a fish population will likely be a function of biological characteristics of the population, sampling gear used, sampling design, and number of samples obtained. While the effects of sampling biases on the accuracy of parameter estimates have received some attention (e.g., Goodyear 1995), precision is less frequently considered. Methods exist for determining requisite precision and associated sample size for certain objectives, such as testing for specified differences between populations or treatments (Desu and Raghavarao 1990). However, the point at which differences are deemed "important" is effectively arbitrary and unlikely related to biological importance (Johnson 1999). Resource managers might need to determine precision required to detect specified "sig-

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nificant" differences to trigger management decisions, although the chosen significance level may be arbitrary. In contrast, researchers doing baseline fisheries biology or descriptive marine ecology should not aim for arbitrary precision levels, but rather should strive to attain the most precise yet cost-effective data possible to maximize the future utility of their results.

Features of tropical reefs pose practical difficulties for researchers. Reef fish assemblages are diverse (Thresher 1991) and coral reef fisheries are characterized by a multispecies catch (Russ 1991). Management requires assessment of multiple stocks, complicating selection of species-specific sample sizes. Additionally, spatially explicit data might be required because reef fishes have a complex spatial structure (e.g., Hart and Russ 1996). This will further restrict potential sample sizes. Finally, the high public profile afforded coral reefs generates social pressure to minimize sampling impacts. This is especially true for research in protected areas (ASTEC 1998), which can provide important insights into anthropogenic effects (e.g., Ferreira and Russ 1995).

Demographic traits of demersal tropical fishes, such as growth parameters, have been estimated with sample sizes ranging from less than 20 (e.g., Dee and Radtke 1989) to greater than 1000 (e.g., Manooch and Hassler 1978). Clearly, more attention to sample size effects on the precision of parameter estimates is needed. We apply a bootstrapping approach, akin to that proposed by Manly (1996), to assessment of precision of parameters of interest to marine ecologists and fisheries biologists (size, age, growth, and mortality parameters). Estimation of multiple parameters enables us to compare the relative precision of different parameters at common sample sizes. We apply the analysis to age–length data sets for four fish species caught in the Great Barrier Reef line fishery, which enables exploration of the effects of underlying population traits, such as longevity and growth trajectory, on precision.

Methods

Data sets analyzed

We used age–length data sets for four species of reef fishes commonly caught on the Great Barrier Reef: *Cephalopholis cyanostigma* (Serranidae), *Lethrinus miniatus* (Lethrinidae), *Lutjanus carponotatus* (Lutjanidae), and *Plectropomus leopardus* (Serranidae) (Fig. 1; Table 1). Real rather than simulated data were used to capture the inherent structure and variation of sampled populations. All data sets represent 1 or 2 years of data collected during fishery-independent sampling programs. The spatial scope of sampling ranges from a single reef (*P. leopardus*) to 24 reefs spanning 7° of latitude (*C. cyanostigma*). While spatial variation is an important focus of the three theses from which the *C. cyanostigma*, *Lethrinus miniatus*, and *Lutjanus carponotatus* data were obtained, our focus is not on the ecology of these species. However, inclusion of data from multiple locations increases the degree of variability in the data sets and makes our results more conservative.

Our data sets span not only four species but also two sampling gears: spear and hook and line. No species was sampled by both gears. Hence, species and gear are confounded and we cannot discern effects due to population biology from those due to gear selectivity. Furthermore, no data exist by which to assess whether the populations have been affected by fishing. Results are therefore interpreted in terms of differences between the *sampled* populations and not those strictly due to real population structure, gear selectivity, and (or) history of exploitation.

The four data sets used in this analysis all contained at least 500 age–length data pairs and were considered by the authors to be large enough to encompass the range of natural variation in the population that could be observed for each species by a given sampling method. This largely subjective assessment, an alternative to which we advocate, was based in part on a cursory review of sample sizes reported in a range of publications on demersal tropical fish growth. A sample size of 500 falls above those used in many studies.

The four sampled populations exhibit diverse characteristics (Fig. 1; Table 1). The *P. leopardus* sample contains the largest fish and the greatest range of sizes but the shortest life span, while the *C. cyanostigma* data contain the smallest maximum size and the most restricted size range but the greatest longevity. The *Lethrinus miniatus*, *P. leopardus*, and *Lutjanus carponotatus* data show decreasing modal age-classes, respectively, and therefore increasing left-hand skew. Data for these species also show a regular decline in age frequencies beyond the modal age-class. In contrast, the *C. cyanostigma* data show no single pronounced mode and no trend of decreasing age frequencies until after age 25.

Preliminary estimates of each species' mean asymptotic size were obtained by taking the average length of the 10 largest fish in each data set (Pauly 1984). We then calculated the percentage of each mean asymptotic size represented by the mean size at 25% of the maximum age. These percentages give an indication of the extent to which each species' growth trajectory reaches a plateau and suggest that *P. leopardus* has less asymptotic growth than the other species. *Cephalopholis cyanostigma*, *Lethrinus miniatus*, and *Lutjanus carponotatus*, on the other hand, all attain approximately three quarters of their mean asymptotic size by one quarter of their maximum age.

Bootstrapping procedure

Random samples ranging in size from 25 to 1000 were drawn with replacement from a given age–length data set. Sampling with replacement implies an assumption that much of the range of variation in the vulnerable population has been captured in the available sample and any additional fish collected would fall within the bounds of our sample. For each sample size, 250 separate random samples were selected. Pilot simulations indicated that estimates of precision did not differ greatly between separate groups of 250 samples, nor did they differ between groups of 250 and 500 or 1000 samples.

Parameter estimation procedures

From each sample, a suite of population parameters was estimated and an age structure was constructed. Parameters included several measures of central tendency (mean length, $\bar{L}$; mean age, $\bar{t}$; modal age, t_{mode}; median age, t_{med}), the estimation of which was straightforward. Due to the multimodal nature of its age structure, modal age was not estimated for *C. cyanostigma*. We also estimated longevity, t_{max}, as the oldest age-class in the sample.

Two von Bertalanffy growth functions (VBGFs) were fitted to each sample by least-squares nonlinear regression of length on age to estimate precision of the Brody growth coefficient, K, and the mean asymptotic length, L_∞. The first set of VBGF parameters, K_u and $L_{\infty,u}$, was estimated with the fitting procedure unconstrained (subscript "u"). However, estimation of VBGF parameters is sensitive to the distribution of sizes and ages in the sample (for an empirical example, see Ferreira and Russ 1994). Often, the youngest and smallest fish will be underrepresented due to sampling biases, irrespective of sample size. We addressed this sample size independent problem by estimating a second set of VBGF parameters from each sample, K_c and $L_{\infty,c}$, constraining (subscript "c") the y-intercept to a reasonable range of settlement sizes for reef fishes

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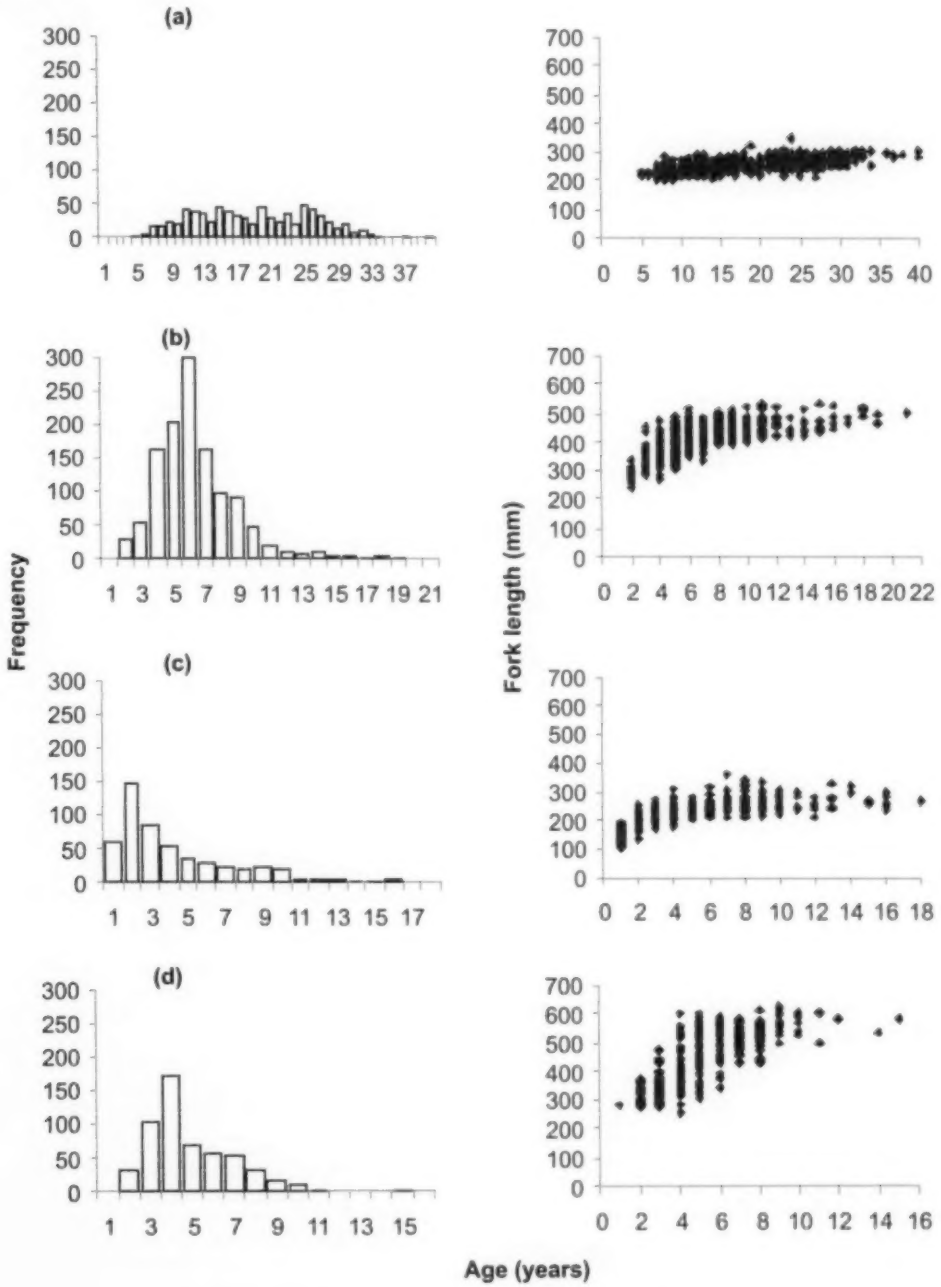
Fig. 1. Age frequency and size at age data for the samples of (*a*) *C. cyanostigma*, (*b*) *Lethrinus miniatus*, (*c*) *Lutjanus carponotatus*, and (*d*) *P. leopardus*.



based on data reviewed by Victor (1991). The validity of these constraints is less important in the present study than the general comparison of constrained versus unconstrained fitting of VBGFs. (Note that the age at theoretical length 0, t_0, is generally of little interest to biologists but does affect estimates of the other two parameters. We do not address the precision of t_0 herein but do indirectly address its influence by constraining the VBGF fits.)

We estimated natural mortality using the method of Pauly (1980) and total mortality using the methods of Ricker (1975) and Hoenig (1983). The regression method proposed by Pauly (1980), which predicts natural mortality from VBGF parameters and water temperature, was used to generate two estimates of the natural mortality rate: $M_{\text{Pauly},u}$ using VBGF parameters estimated by the unconstrained fitting procedure and $M_{\text{Pauly},c}$ using VBGF parameters estimated by the constrained fitting procedure. An estimate of the mean water temperature on the central Great Barrier Reef (26°C) (Lough 1994)

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Table 1. Pertinent characteristics of fishery-independent data sets analyzed in this study.

Species	Sampling gear	Year(s)	Location(s)	n	t_c	t_r	t_{max}	Size range (mm fork length)	$\%L_\infty$ at 25% t_{max}
Cephalopholis cyanostigma	Hook and line	1995–1996	24 reefs spanning 7° latitude, Great Barrier Reef	754	5	12	40	201–353	77
Lethrinus miniatus	Hook and line	1995	18 reefs spanning 3° latitude, Great Barrier Reef	1215	2	6	21	242–534	78
Lutjanus carponotatus	Spear	1997–1998	Palm Island group, central Great Barrier Reef	527	1	2	18	105–360	73
Plectropomus leopardus	Hook and line	1995	Bramble Reef, central Great Barrier Reef	556	1	4	15	257–625	62

Note: n, sample size of original data set; t_c, age at first capture; t_r, first mode in age structure, assumed age at full recruitment to the gear; t_{max}, oldest age-class in the sample; $\%L_\infty$, percentage of mean asymptotic size (L_∞ estimated as the mean size of the 10 largest fish; Pauly 1984). Sources: *C. cyanostigma*: J.W. Mosse (James Cook University, Townsville, Queensland 4811, Australia, unpublished data); *Lethrinus miniatus*: Williams (1997); *Lutjanus carponotatus*: J.P. Kritzer (unpublished data); *P. leopardus*: Effects of Line Fishing Project, CRC Reef Research Centre, James Cook University (unpublished data).

was used in these calculations. The age-based catch curve of Ricker (1975) was used to estimate the total mortality rate, Z_{Ricker}. Catch curves were fitted from the first mode in the age structure of each random sample through to the last age-class before two consecutive frequencies of zero. Here, sample size refers to the number of fish in the sample and not the number of fish actually used in the final catch curve analysis given that fish that fell into age-classes before the first mode and beyond two consecutive zero frequencies were excluded from estimation of Z_{Ricker}. Because the age structure suggested excessive violations of the assumptions of constant recruitment and constant mortality, Z_{Ricker} was not estimated for *C. cyanostigma*. The longevity estimate, t_{max}, was used in Hoenig's (1983) equation to generate a second estimate of total mortality rate, Z_{Hoenig}.

Calculation of precision

Precision is typically defined as the ratio of the standard error of a parameter to the estimate of that parameter (Andrew and Mapstone 1987). However, the standard error is an estimate of the standard deviation of a hypothetical series of parameters estimated using repeated samples (Andrew and Mapstone 1987). Because our simulations produced an actual set of parameters estimated using repeated samples, we used the ratio of the standard deviation of the set of parameter estimates to the mean of those estimates as the estimate of precision. Specifically, we define the precision of parameter x at sample size n as

$$P_{x,n} = \frac{s_{x,n}}{\bar{x}_n}$$

where $s_{x,n}$ is the standard deviation and $\bar{x}_n$ is the mean of the 250 estimates of parameter x at sample size n. This provides a standardized, unitless index that can be compared between different parameters and populations (Andrew and Mapstone 1987).

Precision of predicted age structures was estimated by a modification of the Worthington et al. (1995) D index. Worthington et al. (1995) examined the effects of age determination and sampling errors on accuracy of estimated age structures by using the mean deviation of the proportion in each age-class in a predicted age structure from the proportion in each age-class in the true age structure. Because our focus is on precision rather than accuracy, we used an internal reference derived from the bootstrap data rather than an assumed true external reference. We calculated the deviation of the proportion in an age-class predicted by each random sample from the mean proportion in that age-class over 250 iterations at that sample size. The mean of these individual deviations over 250 iterations was then calculated for each age-class. Finally, precision was calculated as the sum of the mean deviations over all age-classes at that sample size. Specifically, the precision of an age structure estimated from 250 samples of size n is

$$D_n = \sqrt{\sum_{i=1}^{t_{max}} \left(\frac{\sum_{j=1}^{250} (\bar{p}_{i,n} - p_{i,j,n})^2}{250} \right)}$$

where t_{max} is the oldest age-class in the sample, $\bar{p}_{i,n}$ is the mean proportion in age-class i over all 250 samples of size n, and $p_{i,j,n}$ is the proportion of sample j in age-class i at sample size n. This index cannot be compared with precision estimates for other parameters. However, like the P index, it enables comparison of sample size effects on age structure estimation between different populations and can indicate where improvements from additional sampling are minimal.

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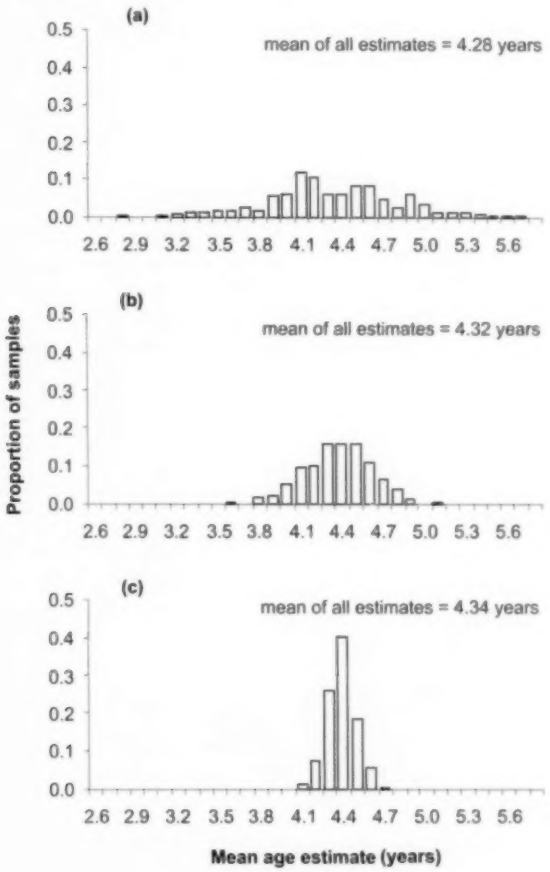
Fig. 2. Example of effects of sample size on the potential range of values that a parameter estimate is likely to take. Distribution of estimates of the mean age of *Lutjanus carponotatus* derived from 250 bootstrapped samples of size (*a*) 50, (*b*) 200, and (*c*) 1000.



Results

The complete set of precision estimates for each species – parameter – sample size combination is presented in the Appendix. Groups of informative results are plotted in Figs. 3–6.

The mean of the estimates of any given parameter was similar across sample sizes, but the variability about the mean of the estimates drastically decreased with increasing sample size (Fig. 2). The effect of this decreasing variability is that improvement in precision associated with increasing sample size for all species–parameter combinations follows a decreasing power function and illustrates the "law of diminishing returns" (Figs. 3–6). In general, to achieve a halving of the P value at a given sample size requires more than tripling that sample size. Despite this general pattern, both relative and absolute improvements in P for a common change in n varied between parameters and, to a lesser extent, species. For example, increasing the sample size from 50 to 100 *Lutjanus carponotatus* will improve the precision of K_u by 0.086, a change of 29% P at $n = 50$. However, the precision of $L_{\infty,u}$ will only improve by 0.033, a 49% change. Similarly, increasing n from 50 to 100 *P. leopardus* will improve the precision of t_{max} by 0.029, a 14% change. An equivalent increase in the number of *C. cyanostigma* samples will only provide an improvement of 0.01, an 11% change.

For all species at all sample sizes, $\bar{L}$ was the most precise parameter estimated. Differences in P values for this parameter at most sample sizes improved by roughly constant amounts from *P. leopardus* to *Lutjanus carponotatus* to *Lethrinus miniatus* to *C. cyanostigma*. Also consistently among the most precise parameters estimated was $\bar{t}$, although at many sample sizes, its precision was still an order of magnitude poorer than that of $\bar{L}$. *Cephalopholis cyanostigma* again exhibited the most precise estimates of this parameter, followed closely by *Lethrinus miniatus* and *P. leopardus* with similar precision levels (Figs. 3*a*, 3*b*, and 3*d*). In contrast, $\bar{t}$ estimates for *Lutjanus carponotatus* across all sample sizes were typically up to twice as imprecise as those for the other species (Fig. 3*c*).

The precision of t_{max} was generally the poorest of any age parameter (Figs. 3*b*–3*d*). The precision of t_{mode} was initially poorer than $\bar{t}$ for all species (with the exception of *C. cyanostigma* for which t_{mode} was not estimated) but became slightly more precise at larger sample sizes and eventually showed no variation (Figs. 3*b*–3*d*). Estimates of t_{med} also showed high precision, reaching 0.01 or less at sample sizes less than 100 for all species (Figs. 3*a*, 3*b*, and 3*d*) except *Lutjanus carponotatus* (Fig. 3*c*).

Not surprisingly, placing constraints upon the fitting process led to more precise VBGF parameter estimates for all species. Parameters estimated by constrained fitting procedures were 2–10 times more precise than those estimated without constraints (Fig. 4). The magnitude of the difference between the two methods was always less for L_∞ than for K (Fig. 4). The estimates of L_∞ were 4–10 times more precise than those of K, with the greatest differences occurring when no constraints were placed upon the fitting process (Fig. 4). Estimates of L_∞ for *P. leopardus* (Figs. 4*b* and 4*d*) and of K for *C. cyanostigma* (Figs. 4*a* and 4*c*) were always the least precise of all species, irrespective of estimation method.

The magnitude of the differences in precision of M_{Pauly} utilizing the two sets of VBGF parameters mirrored the differences in precision between the two VBGF fitting methods, with the actual P values being approximately the average of the precision of the two parameters used in its estimation. Between-species differences likewise mirrored the differences in precision of the growth parameters, with more precise estimates of M_{Pauly} being produced for *Lutjanus carponotatus* and *Lethrinus miniatus*. Similarly, the precision of the Z_{Hoenig} estimator was nearly equivalent to the precision of t_{max}. With few exceptions, these two mortality estimators based on the values of other parameters were generally as or more precise than Z_{Ricker} (Figs. 5*b*–5*d*). Estimates of Z_{Ricker} for *P. leopardus* and *Lutjanus carponotatus* were the most precise (Figs. 5*b* and 5*d*), followed by those for *Lethrinus miniatus* (Fig. 5*c*).

The precision indices for estimated age structures, D, were surprisingly similar among the four species at all sample sizes (Fig. 6). This was the case despite the pronounced difference between the overall character of the *C. cyanostigma*

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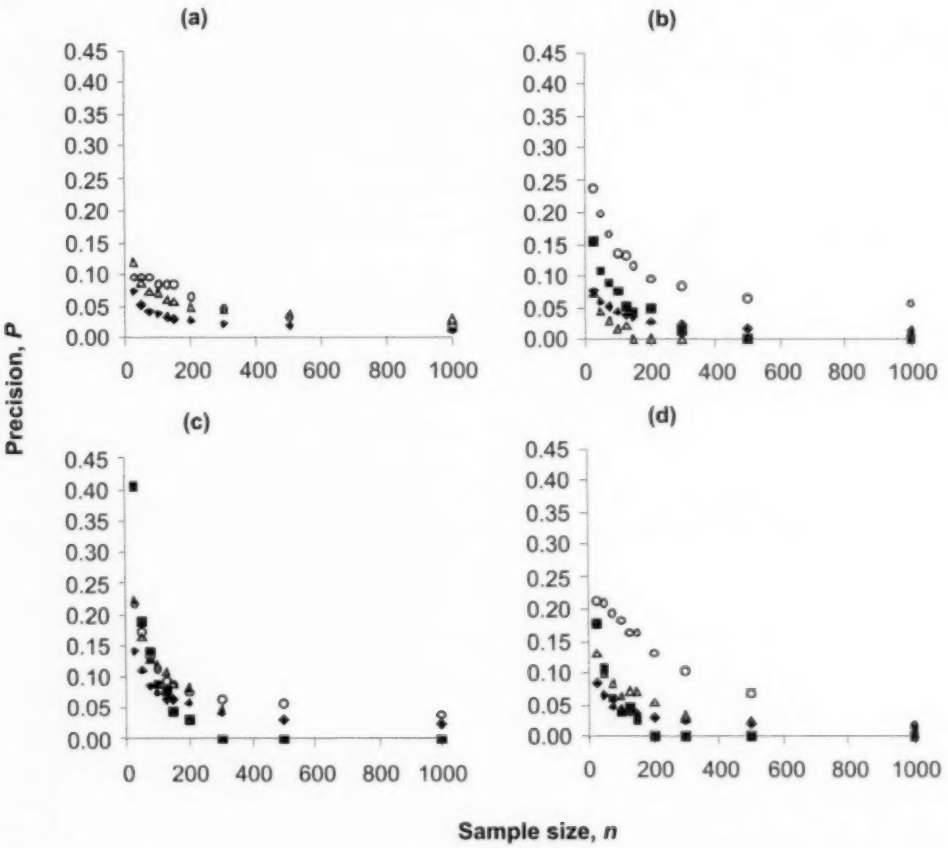
Fig. 3. Precision, *P*, of estimates of the mean age, modal age, median age, and maximum age (i.e., longevity) of (*a*) *C. cyanostigma*, (*b*) *Lethrinus miniatus*, (*c*) *Lutjanus carponotatus*, and (*d*) *P. leopardus* across a range of sample sizes, *n*. The multimodal nature of the *C. cyanostigma* age frequency data meant that modal age estimation was not appropriate. ◆, mean age; ■, modal age; △, median age; ○, maximum age.



age structure and those for the other species and the differing modal and maximum ages between all species (Fig. 1). At small sample sizes, the precision of *C. cyanostigma* age structures was slightly poorer than for the other species, but by a sample size of 200, the four species' *D* values were nearly identical (Fig. 6). The pattern of flattening observed in the *D* versus *n* functions (Fig. 6) was similar to that observed in the various *P* versus *n* functions (Figs. 3–5). The precision of age structures showed steady improvement up to sample sizes of around 150–200 (Fig. 6). Thereafter, more than doubling the sample size from 200 to 500 improved precision by only approximately one third the *D* value at $n = 200$.

Discussion

Length and age parameters

Mean length, mean age, and modal age could consistently be estimated with high precision at small sample sizes relative to other parameters. This can prove useful when managing fisheries with a diverse multispecies catch. Changes in populations of less commercially important species can be monitored by these simpler measures with low data requirements, while the bulk of resources is devoted to more sophisticated parameter estimation for primary target species. The high precision of mean lengths at small sample sizes (i.e., $P << 0.1$ at $n = 25$ for all species) is particularly relevant when data are collected dockside under time constraints amidst unloading of catch (see Gulland 1966).

Growth parameters

Constraining the VBGF fit might be regarded as artificially improving precision by restricting the potential range of values that each parameter can take. There is some truth to this assessment, but it misses the more important point that constraining the VBGF fit is essentially providing additional information not contained in the sample. If the VBGF is an appropriate model for the species in question, this will improve accuracy as well as precision by forcing the curve to better account for changes in size throughout life. Therefore, employing biologically meaningful constraints is likely to result in more accurate estimates and deliver equivalent precision using fewer samples.

The late age at first capture and little curvature in the

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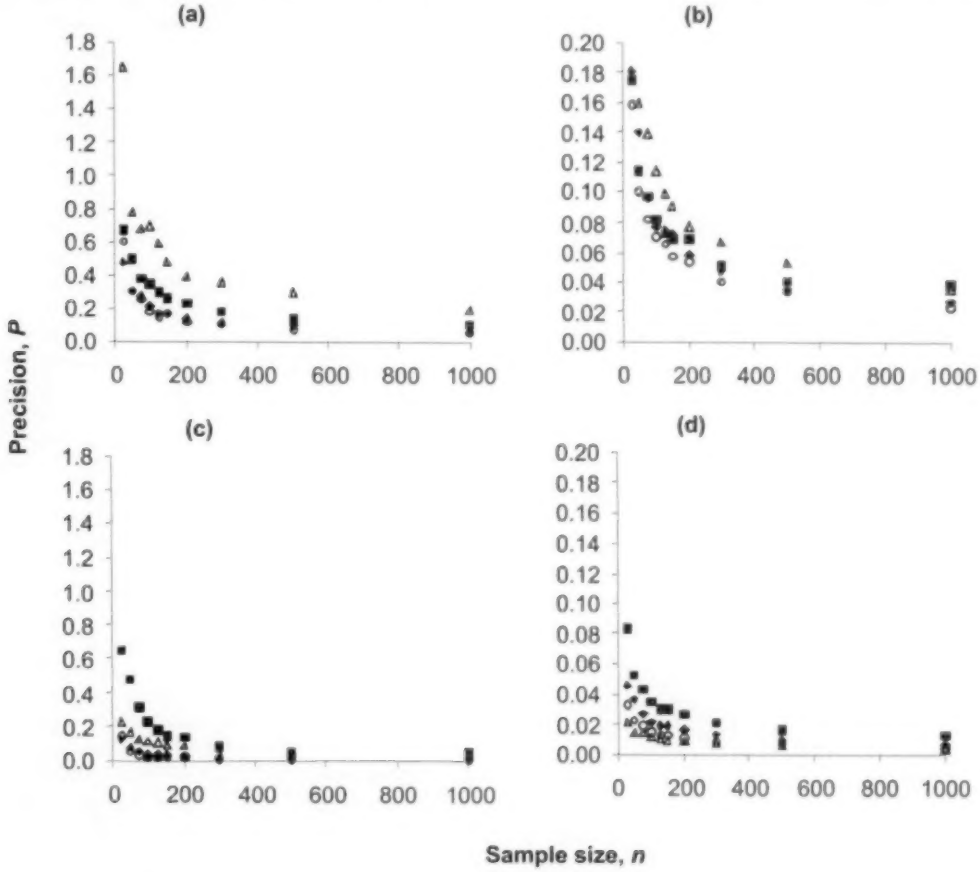
Fig. 4. Precision, *P*, of estimates of the von Bertalanffy growth parameters (*a* and *b*) *K* and (*c* and *d*) L_∞ for four species of coral reef fishes estimated with the *y*-intercept both unconstrained (Figs. 4*a* and 4*c*) and constrained (Figs. 4*b* and 4*d*) across a range of sample sizes, *n*. Precision differed by approximately an order of magnitude between constrained and unconstrained fits, so the left and right plots are presented with different *y*-axis scales. △, *C. cyanostigma*; ○, *Lethrinus miniatus*; ◆, *Lutjanus carponotatus*; ■, *P. leopardus*.



C. cyanostigma data would appear to implicate sampling bias rather than biological traits in the relative imprecision of estimates of *K*. Further supporting this is the comparable precision seen in *K* for the other species, which all have some 1- and (or) 2-year olds represented, despite differing maximum sizes, size ranges, and growth trajectories. In contrast, the precision of L_∞ estimates appears heavily reliant upon underlying biology, as the poorest precision was associated with the least asymptotic growth trajectory (*P. leopardus*). However, sampling biases might also be important here if the selectivity function is domed rather than asymptotic, thereby undersampling larger and older individuals. Alternatively, the lower precision of L_∞ for *P. leopardus* might result because the von Bertalanffy function is not appropriate for the species, which might instead require a nonasymptotic model (Schnute 1981).

Longevity and mortality

Longevity does not appear to be important to its own estimation. Estimates of t_{max} for the longest-lived species, *C. cyanostigma*, were most precise and estimates of t_{max} for the shortest-lived species, *P. leopardus*, were least precise. However, the distribution of fish among older age-classes seems to be important. The ranking of the species from highest to lowest percentage of fish in the last 20% of age-classes is the same as the ranking of t_{max} estimates from most to least precise (i.e., *C. cyanostigma*, *Lutjanus carponotatus*, *Lethrinus miniatus*, *Plectropomus leopardus*). In other words, longevity estimates will be less precise for populations with a comparably thinner "tail" in their age distribution.

On the surface, the results suggest that the regressions of Hoenig (1983) and Pauly (1980) are less data-intensive mortality estimators than the age-based catch curve of Ricker (1975). However, we would be remiss not to briefly consider the question of accuracy before advocating use of any technique. We assumed that for all species, barring *C. cyanostigma*, the catch curve provides the most accurate, if not the most precise, mortality estimate given that it utilizes trends across a range of age-classes rather than one or a few potentially related parameters. We then compared the mean estimates (not presented) obtained by the methods across a range of sample sizes. For *Lutjanus carponotatus*, the Hoenig esti-

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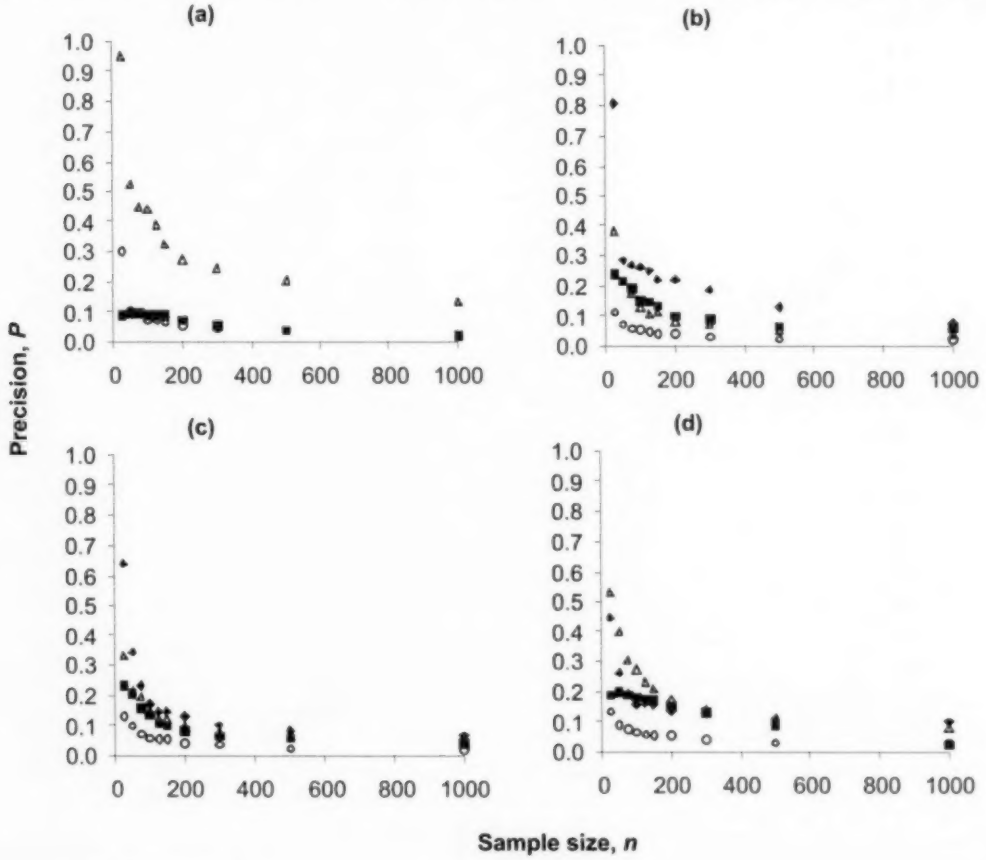
Fig. 5. Precision, *P*, of mortality estimators for (*a*) *C. cyanostigma*, (*b*) *Lethrinus miniatus*, (*c*) *Lutjanus carponotatus*, and (*d*) *P. leopardus* across a range of sample sizes, *n*. Two estimates of natural mortality were generated by Pauly's (1980) equation using von Bertalanffy growth parameters from unconstrained, $M_{Pauly,u}$, and constrained, $M_{Pauly,c}$, growth curve fits. Total mortality was estimated by the age-based catch curve of Ricker (1975), Z_{Ricker}, and by Hoenig's (1983) equation, Z_{Hoenig}. Estimation of Z_{Ricker} is not appropriate for *C. cyanostigma* due to excessive violations of the catch curve assumptions. △, $M_{Pauly,u}$; ○, $M_{Pauly,c}$; ◆, Z_{Ricker}; ■, Z_{Hoenig}.



mate was close to that generated by the catch curve. However, for *P. leopardus* and *Lethrinus miniatus*, the Hoenig estimate was 40% lower than the catch curve estimate. These two species are more heavily fished on the Great Barrier Reef than *Lutjanus carponotatus* (Mapstone et al. 1996). This supports Hoenig's observation that his estimator can underestimate *Z* if fishing changes the skew but not the extent of the age distribution (Hoenig 1983).

Pauly's estimator should produce *M* values that are at most equal and generally less than *Z* estimates. This only occurred for *P. leopardus*. As previously discussed, *P. leopardus* has a growth pattern qualitatively different from those of the other species, perhaps implicating the highly asymptotic nature of the other species' growth in the questionable values of M_{Pauly}. Consideration of L_∞ alone does not account for the length of time spent at the asymptote, but Pauly's equation would estimate similar mortality rates for species with similar growth parameters but differing longevities. These hypotheses require more focused testing and we recommend careful consideration of the effects of population structure prior to use of any mortality estimator.

Age structures

Given that estimating age structures entails replicating entire distributions rather than generating single values, we expected that precision of age structures would improve with increasing sample size more slowly than most parameters. This did not prove to be the case. The explanation might be that the index *D* averages deviations across all age-classes. The effects of substantially overestimating or underestimating a few age frequencies using a given sample might therefore be negated. The remarkably similar *D* values derived at most sample sizes across species and the surprisingly rapid flattening of the *D* versus *n* curve perhaps suggest that an age distribution's general shape can be captured with relatively few samples.

While the basic shape of a distribution can be approximated with relatively few samples, it is important to clearly specify why an age structure is being generated. Approximating the shape of a distribution will not be adequate if the objective involves replicating a recruitment history, in which case, capturing peaks and troughs becomes critical and more samples might be needed (Worthington et al. 1995). On the

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other hand, if the objective is to examine whether fishing has truncated the tail of the distribution (Hilborn and Walters 1992), approximating the general shape may suffice. In fact, objectives might often deal more with specific aspects of the distribution (e.g., modal age), and precision of those particular features should be considered.

Application of the analysis

We did not aim to provide a prescriptive method for sample size determination. Rather, we have explored some factors affecting description of populations, including sample size but also underlying population structure and parameters being estimated. We strongly reiterate that an appropriate sample size can only be specified by consideration of resource expenditure per sample collected and (or) the degree of precision required to achieve specific objectives.

Still, some general comments on sample size requirements for baseline or descriptive studies can be made. As n increases and P decreases, one must sample more and more to gain less and less. For most parameters examined, relative improvements above sample sizes of around 300 were negligible unless the increase was on the order of several hundred. Absolute improvements were always minimal. Unfortunately, the question becomes more difficult at the lower end of the sample size spectrum where attention of researchers is more likely to be focused as they try to minimize costs. For most parameters, the P (or D) versus n function appeared very steep up to a sample size of at least 100 and began to appear quite flat by sample sizes of around 150–200. General rules for minimum sample sizes when statistically comparing frequency distributions range from an average of 5–10 observations per category (Sokal and Rohlf 1981). In light of our results, an average of 7–10 fish per age-class would be a useful although possibly overly conservative guideline for estimating age structures and a variety of parameters for all but those species living more than 25 or 30 years. Longer-lived species might require fewer samples per age-class. By our guideline, the target sample size for *C. cyanostigma* would be 400, which would not appreciably improve precision of most parameters from a sample half that size. Such exceptions highlight the limitations of general rules.

We used data sets in hand and retrospectively assessed different hypothetical samples. It might seem fruitless for other investigators to conduct similar analyses if samples need to have been collected first. However, one advantage of bootstrapping methods is their potential to build large numbers of hypothetical samples from relatively small amounts of data (Manly 1996). While extrapolating from small data sets is not without risk, our minimum sample size of 500 for the simulation data sets was excessively strict in light of our results. A modest pilot sample could roughly capture the population's characteristics and help determine the additional sampling required to attain more precise estimates.

Alternatively, extant data sets for species similar to focal species can also be used to approximate the population in question. For example, one species used herein, *Lutjanus carponotatus*, exhibits demographic traits similar to the congeneric *Lutjanus adetii* on the Great Barrier Reef (Newman et al. 1996). Data for this species could have been used as an initial approximation of a *Lutjanus carponotatus* population had data for *Lutjanus carponotatus* been unavailable. This could lead to additional sampling if the newly researched population is revealed to be substantially different from the proxy population.

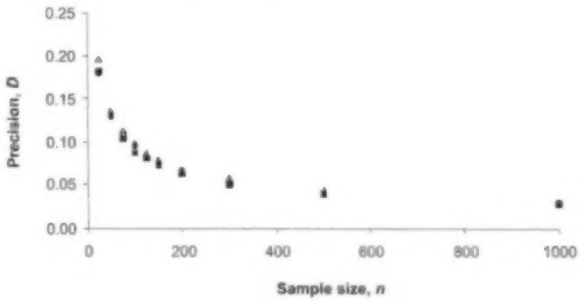

Fig. 6. Precision, D, of estimated age structures for four species of coral reef fishes across a range of sample sizes, n. △, *C. cyanostigma*; ○, *Lethrinus miniatus*; ◆, *Lutjanus carponotatus*; ■, *P. leopardus*.

Sample size and (or) sampling method can be beyond the researcher's control, particularly when using fishery-dependent samples. In such cases, an analysis like ours can aid the researcher in assessing what parameters can be reliably estimated from a sample. For example, if a fisher provided a sample of 50 fish, mean age and length might be confidently estimated. Little faith would be placed in K estimates and corresponding M_{Pauly} estimates.

Future directions

The effects of sample size on the precision of descriptive parameters, such as density or mean size of organisms, have received previous attention (e.g., Andrew and Mapstone 1987; Downing 1989; Garner 1997). In contrast, precision of vital rate parameters, such as those related to growth and mortality, has largely been ignored (but see Jensen 1996). Given that such parameters are crucial to understanding the functioning and dynamics of ecological systems (Ebert 1999) and as such form central components of fisheries stock assessments (Hilborn and Walters 1992), our study can make an important contribution to both pure and applied marine ecology. A logical progression would be estimation of precision and associated sample sizes required to achieve objectives ranging from statistical comparisons of desired power to modeling with desired sensitivity. We stress that any selected target precision is essentially arbitrary unless project-specific objectives and real sampling costs (Downing 1989) are defined and related to precision. At the very least, consideration of these results or, better still, application of similar analyses to context-specific data should lead to more precise yet cost-effective parameter estimation with minimal impact on the population under study.

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Appendix

Table A1. Precision of population parameter estimates for four coral reef fish species across a range of sample sizes.

	n									
	25	50	75	100	125	150	200	300	500	1000
Cephalopholis cyanostigma										
$\bar{L}$	0.014	0.012	0.010	0.008	0.007	0.006	0.006	0.005	0.004	0.003
$\bar{t}$	0.074	0.052	0.042	0.038	0.032	0.029	0.026	0.021	0.018	0.011
t_{mode}	na	na	na	na	na	na	na	na	na	na
t_{med}	0.119	0.088	0.074	0.070	0.061	0.056	0.050	0.043	0.038	0.030
t_{max}	0.095	0.095	0.095	0.085	0.084	0.083	0.066	0.046	0.033	0.017
K_u	1.651	0.774	0.679	0.693	0.588	0.478	0.391	0.357	0.294	0.191
$L_{\infty,u}$	0.226	0.163	0.122	0.109	0.102	0.089	0.080	0.071	0.054	0.039
K_c	0.632	0.160	0.139	0.115	0.100	0.092	0.078	0.067	0.053	0.035
$L_{\infty,c}$	0.021	0.014	0.014	0.011	0.010	0.010	0.008	0.007	0.005	0.004
$M_{Pauly,u}$	0.951	0.523	0.449	0.444	0.392	0.325	0.274	0.245	0.204	0.135
$M_{Pauly,c}$	0.301	0.106	0.093	0.077	0.067	0.062	0.053	0.045	0.036	0.024
Z_{Ricker}	na	na	na	na	na	na	na	na	na	na
Z_{Hoenig}	0.090	0.091	0.095	0.086	0.086	0.087	0.071	0.051	0.036	0.018
Lethrinus miniatus										
$\bar{L}$	0.022	0.017	0.015	0.012	0.010	0.010	0.009	0.007	0.005	0.004
$\bar{t}$	0.075	0.060	0.051	0.043	0.038	0.035	0.028	0.024	0.017	0.013
t_{mode}	0.153	0.110	0.089	0.077	0.051	0.044	0.048	0.015	0	0
t_{med}	0.074	0.045	0.030	0.017	0.021	0	0	0	0	0
t_{max}	0.238	0.197	0.164	0.135	0.133	0.118	0.095	0.083	0.065	0.057
K_u	0.604	0.309	0.256	0.183	0.152	0.165	0.119	0.102	0.073	0.053
$L_{\infty,u}$	0.147	0.047	0.035	0.024	0.020	0.021	0.016	0.013	0.010	0.007
K_c	0.159	0.101	0.082	0.070	0.065	0.058	0.054	0.041	0.034	0.024
$L_{\infty,c}$	0.032	0.022	0.018	0.015	0.013	0.013	0.011	0.009	0.007	0.005
$M_{Pauly,u}$	0.386	0.215	0.175	0.125	0.105	0.113	0.082	0.070	0.050	0.037
$M_{Pauly,c}$	0.111	0.071	0.058	0.050	0.046	0.041	0.038	0.029	0.024	0.017
Z_{Ricker}	0.809	0.286	0.266	0.263	0.249	0.224	0.222	0.187	0.126	0.075
Z_{Hoenig}	0.240	0.212	0.194	0.149	0.148	0.134	0.101	0.087	0.066	0.059
Lutjanus carponotatus										
$\bar{L}$	0.036	0.027	0.022	0.018	0.015	0.015	0.015	0.011	0.008	0.006
$\bar{t}$	0.143	0.112	0.086	0.075	0.063	0.065	0.057	0.042	0.031	0.024
t_{mode}	0.405	0.189	0.141	0.088	0.077	0.045	0.032	0	0	0
t_{med}	0.222	0.163	0.129	0.119	0.108	0.089	0.083	0.049	0	0
t_{max}	0.216	0.172	0.134	0.115	0.093	0.088	0.076	0.064	0.058	0.038
K_u	0.469	0.300	0.274	0.214	0.173	0.172	0.136	0.113	0.094	0.064
$L_{\infty,u}$	0.127	0.068	0.052	0.035	0.030	0.031	0.024	0.019	0.016	0.011
K_c	0.181	0.141	0.096	0.078	0.075	0.073	0.058	0.048	0.035	0.026
$L_{\infty,c}$	0.045	0.036	0.027	0.021	0.019	0.019	0.016	0.013	0.009	0.007
$M_{Pauly,u}$	0.330	0.214	0.192	0.148	0.121	0.120	0.094	0.078	0.066	0.044
$M_{Pauly,c}$	0.129	0.100	0.070	0.056	0.053	0.052	0.042	0.035	0.025	0.019
Z_{Ricker}	0.638	0.342	0.231	0.171	0.147	0.144	0.128	0.100	0.079	0.065
Z_{Hoenig}	0.235	0.201	0.171	0.131	0.102	0.098	0.081	0.065	0.059	0.042
Plectropomus leopardus										
$\bar{L}$	0.044	0.032	0.025	0.023	0.019	0.018	0.016	0.013	0.010	0.007
$\bar{t}$	0.083	0.064	0.047	0.042	0.039	0.035	0.029	0.025	0.019	0.014
t_{mode}	0.176	0.106	0.059	0.039	0.047	0.027	0	0	0	0
t_{med}	0.129	0.097	0.085	0.063	0.071	0.070	0.054	0.033	0.024	0
t_{max}	0.210	0.209	0.193	0.180	0.161	0.163	0.131	0.104	0.067	0.019
K_u	0.669	0.494	0.380	0.345	0.293	0.266	0.229	0.180	0.136	0.102
$L_{\infty,u}$	0.656	0.482	0.313	0.228	0.174	0.146	0.135	0.084	0.052	0.038

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Table A1 (*concluded*).

	n									
	25	50	75	100	125	150	200	300	500	1000
K_c	0.175	0.115	0.097	0.819	0.073	0.069	0.069	0.052	0.041	0.038
$L_{\infty,c}$	0.084	0.052	0.043	0.035	0.031	0.030	0.027	0.021	0.016	0.013
$M_{\text{Pauly.u}}$	0.531	0.399	0.302	0.271	0.231	0.208	0.177	0.139	0.103	0.077
$M_{\text{Pauly.c}}$	0.136	0.089	0.074	0.063	0.056	0.053	0.052	0.039	0.031	0.029
Z_{Ricker}	0.448	0.262	0.193	0.159	0.165	0.157	0.133	0.127	0.112	0.099
Z_{Hoenig}	0.189	0.197	0.186	0.183	0.167	0.174	0.151	0.127	0.086	0.024

Note: Precision is defined as the ratio of the standard deviation of 250 distinct parameter estimates to the mean of those same estimates. n, sample size; $\bar{L}$, mean fork length; $\bar{t}$ mean age; t_{mode}, modal age-class; t_{med}, median age-class; t_{max}, maximum age-class; K_u, von Bertalanffy growth coefficient, estimated with y-intercept unconstrained; $L_{\infty,u}$, von Bertalanffy mean asymptotic size, estimated with y-intercept unconstrained; K_c, von Bertalanffy growth coefficient, estimated with y-intercept constrained; $L_{\infty,c}$, von Bertalanffy mean asymptotic size, estimated with y-intercept constrained; $M_{\text{Pauly.u}}$, natural mortality rate estimated by Pauly's (1980) regression using von Bertalanffy parameters from unconstrained fit; $M_{\text{Pauly.c}}$, natural mortality rate estimated by Pauly's (1980) regression using von Bertalanffy parameters from constrained fit; Z_{Ricker}, total mortality rate estimated by Ricker's (1975) catch curve; Z_{Hoenig}, total mortality rate estimated by Hoenig's (1983) regression; na, features of the age structure meant that estimation of these parameters was not appropriate.

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Hierarchical Bayesian models of length-specific catchability of research trawl surveys

Shelton J. Harley and Ransom A. Myers

Abstract: To estimate absolute abundance from research trawl surveys, the catchability of the fish to the gear must be known or estimated. Using 47 data sets of length-specific catchability, we conducted a hierarchical Bayesian meta-analysis of length-specific catchability for a number of different species groups. It was found that the Bayesian estimates of catchability were seldom near or above 1 for any species or size. This suggests that any assumption that swept-area abundance estimates are in fact absolute abundance would likely underestimate the true abundance. Catchability was higher for haddock (*Melanogrammus aeglefinus*) than for Atlantic cod (*Gadus morhua*) of the same size, suggesting behavioural differences between these two species. We found a seasonal difference in catchability with higher catchability for surveys in summer–fall than for those in spring–winter. The results of this study can be applied both for the reconstruction of fish community structure for ecosystem models and as auxiliary (or prior) information for single-species stock assessment where catchability is estimated within the stock assessment procedure.

Résumé : Il faut connaître ou estimer la capturabilité des poissons en fonction l'engin de pêche pour pouvoir estimer l'abondance absolue à partir de données d'inventaires scientifiques faits au chalut. À l'aide de 47 séries de données de capturabilité d'après la longueur, nous avons fait une méta-analyse hiérarchique bayésienne de la capturabilité d'après la longueur chez plusieurs groupes spécifiques. Les estimations bayésiennes sont rarement près de 1 ou supérieures à 1 pour quelque espèce ou taille que ce soit. Donc, en supposant que les estimations de l'abondance sur la surface échantillonnée représentent la véritable abondance absolue on sous-estime l'abondance réelle. La capturabilité est plus grande pour l'Aiglefin (*Melanogrammus aeglefinus*) que pour la Morue (*Gadus morhua*) franche de même taille, ce qui suppose des différences de comportement entre les deux espèces. Il existe des différences saisonnières dans la capturabilité, les valeurs étant plus grandes en été et en automne qu'au printemps et en hiver. Les résultats de notre étude peuvent s'appliquer à la reconstitution de la structure de la communauté icthyenne pour utilisation dans les modèles d'écosystèmes et servir de données auxiliaires (ou a priori) pour l'évaluation de stocks monospécifiques, lorsque la capturabilité est estimée par des procédures d'évaluation des stocks.

[Traduit par la Rédaction]

Introduction

To assess and understand changes in ecosystems, scientific surveys are often carried out to estimate abundance of species. However, before we can best use these survey results, we must translate the estimates to absolute abundance. Two fundamental difficulties with most scientific surveys are that not all sizes and species are caught equally efficiently by the survey gear and that it is difficult to translate from an index to an estimate of absolute abundance. Both of these problems occur for research trawl surveys, which are the most common approach used to obtain fishery-independent estimates of abundance. However, it is sometimes possible to estimate the efficiency of research trawl surveys either from remote sensing (Somerton et al. 1999) or by comparing survey estimates with absolute abundance obtained from catch-age analyses (Sparholt 1990). Unfortunately, only a few reliable estimates from experiments are available and catch-age analyses are usually carried out only for the most valuable commercial species. Thus, we have no estimates for the majority of species caught in research surveys.

In order to provide improved abundance estimates needed for ecosystem models of the marine environment, provide priors for catchability needed for stock assessments, and provide a baseline for non-Bayesian assessments, we have carried out a meta-analysis of the most reliable 47 marine bottom trawl research surveys that we could obtain from around the world.

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Estimating catchability

In general, catchability describes how the abundance and size composition of a species differs between the population and the survey catch. The estimate of catchability is the value required to scale the survey estimate of abundance to absolute abundance. We can define absolute abundance N_l of length-class l:

$$(1) \qquad N_l = q_l c_l \frac{A}{a}$$

where q is the catchability scalar, c is the mean catch per tow, a is the area swept by one trawl tow, and A is the total survey area. When abundance is measured as the biomass, this leads to $c\frac{A}{a}$ being referred to as the "area-swept bio-

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mass estimate." It is also often know as "trawlable biomass" or as "minimum trawlable biomass." This last term is misleading in instances where catchability is greater than 1, as the area-swept biomass estimate will overestimate the actual biomass.

Most previous attempts to scale research surveys involved transforming relative indices of abundance to absolute abundance using a single species-specific scalar. This is done by scaling the total abundance of the species caught in the survey to that in the ocean. These estimates do not utilize information on the length/age structure of the population or the length/age-specific selectivity of the survey gear. We call this a "bulk estimate" as opposed to the length-specific catchability estimates that we present here.

The catchability process can be described by three components as suggested by Edwards (1968): (*i*) availability to the gear (the vertical distribution of the species), (*ii*) vulnerability (including herding effects, net avoidance, and mesh selectivity), and (*iii*) spatial/seasonal factors (the spatial distribution of the fish in the trawlable and untrawlable regions). The vertical distribution of a number of species has been found to vary with time of day (Casey and Myers 1998). Fish behaviour in and around trawl gear is known to influence vulnerability (Wardle 1983) as well as mesh size and the size of the catch (Suuronen and Millar 1992; Godø et al. 1999). This second component encompasses the more general field of gear selectivity, which includes the properties of both commercial and survey gears. While the approach in the field of gear selectivity has used direct observational studies and experiments, our approach here is indirect where all three components of catchability are considered together.

The interpretation of an estimate of catchability is simplified by the calculation of expected density D of fish:

$$(2) \quad D = N/A$$

which, when scaled to account for the area-swept by the tow (a), leads to an expected catch rate c^*. Thus, catchability is the observed catch rate divided by the expected catch rate:

$$(3) \quad q = c/c^*$$

Catchability less than 1 indicates that less fish were caught than predicted in the path (assumed here to be the width of the net opening) of the trawl; conversely, catchability greater than 1 indicates that more fish were caught than predicted to occupy the area trawled. Catchability could be greater than 1 if the trawl gear was able to herd fish into the path of the net or if the calculation of area-swept abundance involved extrapolations to untrawlable regions where the density of fish was lower (than the surveyed region). Understanding these processes has important consequences for the interpretation of survey indices and subsequent management decisions (Godø and Walsh 1992; Somerton et al. 1999).

Edwards (1968) considered each of the three components of catchability described above to assign catchability estimates for a number of species found off the New England coast. Sparholt (1990) used estimates of catchability for a number of species from multispecies Virtual Population Analysis (MVPA) to obtain estimates of catchability from 10 species from the North Sea. To obtain estimates of catchability for other North Sea species, Sparholt (1990) then applied to each of the other species an estimate for one of the 10 species for which catchability had been estimated. The assignment was based on morphological and behavioural similarities between species. Casey (2000) used the estimates from Edwards (1968) and applied a correction for diel variability in catchability to allow the reconstruction of absolute abundance for different fish groups on the Southern Grand Bank. These studies used a single scalar for catchability and thus ignored the length-specific processes that are known to influence gear selectivity.

The length-specific estimates developed here have three main advantages over the bulk estimates. First, they allow separate consideration of adult and juveniles. A single bulk estimate would scale up both adult and juvenile survey abundance the same. This leads to difficulties in estimating natural or total mortality. Second, in instances where there are large changes in the size composition of the population, a single bulk catchability will introduce extra bias into estimates of absolute abundance. Third, it is simpler to assign estimates of catchability to other species. For example, with a single bulk estimate, it is difficult to assign estimates of catchability across species from the family if there are large differences in size (such as large and small gadoids). Estimates of length-specific catchability overcome this difficulty.

We collected estimates of research trawl survey catchability from stock assessments worldwide. We used hierarchical models that incorporate information from other data sets to provide improved estimates for a single data set as well as the standard nonhierarchical techniques that assume that the only information on catchability-at-length for a given data set is contained within the data set. Multiple estimates for the same or similar species were combined using hierarchical Bayesian techniques to obtain metaanalytical estimates of catchability-at-length (and associated uncertainty) for a number of species groups. We propose that results of this analysis could be used both as auxiliary information (or "priors") in stock assessment models and to assist in the reconstruction of fish community structure from trawl survey time series (e.g., Sparholt 1990; Casey 2000). As one application, we describe how a number of species from the Scotian Shelf off the eastern coast of Canada can be assigned estimates of catchability based on morphological and behavioural similarities with species where meta-analytical estimates of catchability were determined.

Methods and materials

Data used for meta-analysis

We attempted to compile all of the data worldwide on research trawl catchability. We focused on four regions: New Zealand, the North Sea, and the east and west coasts of North America. We compiled 66 data sets with length/age-specific catchability estimates for 21 species where the following criteria were met: (*i*) an age-structured (or length-structured) stock assessment was performed using research trawl survey data, (*ii*) the survey covered all, or most, of the stock assumed for modeling purposes, and (*iii*) there were sufficient length/age-classes to allow the fitting of a logistic curve to the data. A further nine data sets that had insufficient data for curve fitting were used to estimate bulk catchability (Harley et al. 2001). Estimates of catchability were obtained from published and unpublished stock assessment reports produced by fisheries management bodies. Stock assessment scientists were contacted directly when extra details or clarification was required.

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Here, the sample unit or data set consisted of catchability estimates for a population from a survey. Where multiple research surveys had been conducted, several data sets were available for a single population. All trawl surveys were designed incorporating a random stratified sampling strategy, although for some surveys (e.g., English Groundfish Survey), the stations are not rerandomized each year. For all data sets, we collected the catchability estimates at age (or size), estimates of uncertainty (when available), biological parameters to allow the transformation of age to length, and details of the survey used (these data are available from the corresponding author).

For the current analysis of length-specific catchability, only 47 of the data sets representing 11 species were used (Table 1). We eliminated two data sets that had length-specific catchability curves with a strong descending right-hand limb, as this pattern was inconsistent with the logistic curve used in the meta-analysis. These were for Atka mackerel (*Pleurogrammus monopteryguis*) and Pacific cod (*Gadus macrocephalis*) from the Bering Sea and the Gulf of Alaska, respectively. Five flatfish data sets from Bering Sea surveys were excluded because the seafloor characteristics and gear types were not comparable with the majority of the data. The flatter bottom in the Bering Sea results in reduced probability of escape below the ground gear and thus higher estimates of catchability (D. Somerton, National Marine Fisheries Service (NMFS), 7600 Sand Point Way NE, Seattle, Wash., personal communication). One data set for yellowtail flounder (*Pleuronectes ferrugineus*) from southern New England was excluded, as the survey gear was specifically set up to target flatfish (S. Cadrin, NMFS, 166 Water Street, Woods Hole, Mass., personal communication) and was not comparable with the other yellowtail flounder data sets. Five data sets were excluded because of unrealistic catchability estimates (many greater than five). Three of these were for the New Zealand red cod (*Pseudophycis bachus*). The assessments for these stocks were the first to be conducted and the catchability estimates were extremely high and the assessments were quite uncertain. The other two data sets that were excluded were for American plaice (*Hippoglossoides platessoides*) in Northwest Atlantic Fisheries Organization (NAFO) areas 3LNO (Morgan et al. 1999) and 4T (Marin et al. 1998) where the catchability estimates were around 4. Estimates of catchability for Pacific ocean perch (*Sebastes alutus*) and shortspine thornyhead (*Sebastolobus alascanus*) were considered unreliable after discussions with stock assessment scientists (J. Ianelli and A. Hollowed, NMFS, 7600 Sand Point Way NE, Seattle, Wash.). The research surveys and stock definition for these assessments are undergoing revisions. In all cases, it would be possible to include these unusual data sets in the analysis and the metaanalytical framework could be used to obtain perhaps better estimates for these data, but it was felt that including them would only serve to unrealistically increase the uncertainty in the meta-analytic estimates of catchability.

The data were divided into seven groups for the hierarchical modeling (Table 2). The two gadoid groups include species from the order Gadiformes. Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) were modeled both individually and combined as demersal gadoids. The combined analysis was performed to allow the allocation of catchability estimates from this group to other species. The demersal gadoid group also included whiting (*Merlangius merlangus*). The pelagic gadoid group included two New Zealand species, hoki (*Macruronus novaezelandiae*) and hake (*Merluccius australis*), pollock (or saithe) (*Pollachius virens*) from the North Sea, walleye pollock (*Theragra chalcogramma*) from the Bering Sea, and silver hake (*Merluccius bilinearis*) from the Scotian Shelf.

New Zealand ling (*Genypterus blacodes*) were considered as a separate group. Ling is an elongated eel-shaped fish that generally feeds at the bottom on crustaceans and fish (Annala et al. 1999). It lives to about 30 years, with females obtaining lengths of 160 cm. The Chatham Rise trawl survey catches ling of all ages (S.J. Harley, personal observation). This species should be useful for providing estimates for species such as wolffish and eelpout.

It was difficult to determine which species to include in the flatfish group. All of the Bering Sea data sets were excluded as noted above, and many of the assessments with very high catchability estimates were for flatfish species. The data used in the analysis comprised six data sets for yellowtail flounder and two for American plaice.

Length-specific catchabilities

Length-specific catchabilities were derived from catch-at-age analyses. There are two approaches to catch-at-age analyses: (*i*) traditional Virtual Population Analysis (VPA) methods that assume that catch-at-age is known exactly and estimate catchability-at-age for each year and (*ii*) methods that assume error in the catch-at-age data and estimate a single age-specific selectivity curve for each gear/research vessel type. Estimates derived from both modeling approaches were used here.

The traditional VPA (and its extensions) assumes that the catch-at-age is known without error and uses research survey data to "tune" the analysis to estimate the number of survivors in the last year and the fishing mortality. In order to carry out these estimates, it is also necessary to estimate catchability-at-age. It is usually assumed that estimation errors are lognormal, i.e.:

$$S_{ta} = q_a N_{ta} e^{\varepsilon_{ta}}$$

where $\varepsilon_{ta} \sim N(0, \sigma^2)$, N_{ta} is the estimated number of fish at age a in year t from the VPA, q_a is the catchability-at-age a for the survey, S_{ta} is the survey estimate of the numbers, and ε_{ta} is the estimation error. The log catchability Q_a is estimated using a simple average:

$$\hat{Q}_a = \sum_{t=1}^{T} (\log(N_{ta}) - \log(S_{ta})) / T$$

with the usual standard error.

An alternative approach is to estimate a single age- or length-specific selectivity curve for each survey series. In this case, a more complex objective function is minimized. Here, we need to consider two parts of the relationship. First, the total biomass for a species is estimated from the survey in each year, B_t, and this is compared with the biomass predicted by the model, again usually assuming a lognormal error term, i.e.:

$$B_t = \left(\sum_a N_{ta} q w_a s_a \right) e^{\varepsilon_t}$$

where $\varepsilon_t \sim N(0, \sigma^2)$, w_a is average weight-at-age, and the survey catchability q is assumed to be constant for each survey.

In a separate likelihood, the proportion of fish caught in a survey of age a in a given year is used to estimate the selectivity at age s_a (often standardized to a maximum of 1), typically by assuming that the proportion at age follows a multinomial or related distribution. In this case, the estimate of catchability-at-age is

$$\hat{q}_a = \hat{q}\hat{s}_a$$

Estimates of catchability-at-age were converted to catchability-at-length using a von Bertalanffy growth function. A single curve was used for each population.

Catchability models

Millar (1995) described seven different functional forms for modeling hook and gillnet selectivity that provide a starting point for our analysis. As part of our initial exploratory analysis of the

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Table 1. Catchability data used in the meta-analysis.

Species/stock	Survey	Source
Atlantic cod (*Gadus morhua*)		
NAFO 2J+3KL (Labrador and N. Grand Bank)	Fall	Shelton et al. 1996
NAFO 3NO (S. Grand Bank)	Fall	Davis et al. 1996
NAFO 3NO (S. Grand Bank)	Spring (a), Canadian	Davis et al. 1996
NAFO 3NO (S. Grand Bank)	Spring (b), U.S.S.R.	Davis et al. 1996
NAFO 3Ps (St. Pierre Bank)	Spring	Brattey et al. 1999
NAFO 3Ps (St. Pierre Bank)	Winter, French	Brattey et al. 1999
NAFO 4T (St. Lawrence)	Fall	Chouinard et al. 1999
NAFO 4Vn (Sydney Bight)	Summer	Mohn et al. 1998*b*
NAFO 4VsW (E. Scotian Shelf)	Spring	Mohn et al. 1998*a*
NAFO 4VsW (E. Scotian Shelf)	Summer	Mohn et al. 1998*a*
NAFO 5Z (Georges Bank)	Fall	O'Brien and Cadrin 1999
NAFO 5Z (Georges Bank)	Spring (a), Yankee 36	O'Brien and Cadrin 1999
NAFO 5Z (Georges Bank)	Spring (b), Yankee 41	O'Brien and Cadrin 1999
NAFO 5Y (Gulf of Maine)	Fall	Mayo 1998
NAFO 5Y (Gulf of Maine)	Spring	Mayo 1998
ICES IV and IIIa (North Sea and Skaggerak)	Fall (EGFS)	ICES 199
ICES IV and IIIa (North Sea and Skaggerak)	Winter (IBTS)	ICES 1999
Haddock (*Melanogrammus aeglefinus*)		
NAFO 4TVW (St. Lawrence and Scotian Shelf)	Summer	Frank et al. 1997
NAFO 4X (Browns Bank)	Summer	Hurley et al. 1999
ICES IV and IIIa (North Sea and Skaggerak)	Fall (EGFS)	ICES 1999
ICES IV and IIIa (North Sea and Skaggerak)	Winter (IBTS)	ICES 1999
NAFO 5Z (Georges Bank)	Fall	Gavaris and Van Eeckhaute 1998
NAFO 5Z (Georges Bank)	Spring (a), Yankee 36	Gavaris and Van Eeckhaute 199
NAFO 5Z (Georges Bank)	Spring (b), Yankee 41	Gavaris and Van Eeckhaute 1998
NAFO 5Z (Georges Bank)	Spring (c), Canadian	Gavaris and Van Eeckhaute 1998
Whiting (*Merlangius merlangus*)		
ICES IV and IIIa (North Sea and Skaggerak)	Fall (EGFS)	ICES 1999
ICES IV and IIIa (North Sea and Skaggerak)	Winter (IBTS)	ICES 1999
Hake (*Merluccius australis*)		
NZ HAK1 (Subantarctic)	Fall	Dunn et al. 2000
NZ HAK1 (Subantarctic)	Spring	Dunn et al. 2000
NZ HAK4 (Chatham Rise)	Summer	Dunn et al. 2000
Hoki (*Macruronus novaezelandiae*)		
NZ HOK1	Summer (a), Chatham Rise	Cordue 2000
NZ HOK1	Fall (Subantarctic)	Cordue 2000
NZ HOK1	Summer (b), Southland	Cordue 2000
Silver hake (*Merluccius bilinearis*)		
NAFO 4VWX (Scotian Shelf)	Summer	Showell 1998
Pollock (*Pollachius virens*)		
ICES IV and IIIa (North Sea and Skaggerak)	Fall (EGFS)	ICES 1999
Walleye pollock (*Theragra chalcogramma*)		
E. Bering Sea	Fall (AFSC)	J. Ianelli (NMFS, 7600 Sand Point Way NE, Seattle, Wash., unpublished data)
American plaice (*Hippoglossoides platessoides*)		
NAFO 5Y (Gulf of Maine)	Fall	O'Brien et al. 1999
NAFO 5Y (Gulf of Maine)	Spring	O'Brien et al. 1999
Yellowtail flounder (*Pleuronectes ferrugineus*)		
Cape Cod (Ccod)	Fall	Cadrin 2000*a*
Cape Cod (Ccod)	Spring	Cadrin 2000*a*
NAFO 5Z (E. Georges Bank)	Fall	Cadrin 2000*b*
NAFO 5Z (E. Georges Bank)	Spring	Cadrin 2000*b*
S. New England (SNE)	Fall	Cadrin 2000*c*
S. New England (SNE)	Spring	Cadrin 2000*c*
Ling (*Genypterus blacodes*)		
NZ LIN3&4 (Chatham Rise)	Summer	Horn et al. 2000
NZ LIN5&6 (S. Plateau)	Fall	Horn et al. 200
NZ LIN5&6 (S. Plateau)	Spring	Horn et al. 2000

Note: NAFO, Northwest Atlantic Fisheries Organization; ICES, International Council for the Exploration of the Sea; EGFS, English Groundfish Survey; IBTS, International Bottom Trawl Survey; NZ, New Zealand; AFSC, Alaska Fisheries Science Center.

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Table 2. Groupings and numbers of data sets used for the hierarchical meta-analysis.

Group/species	Common name	Data sets
Atlantic cod		
Gadus morhua	Atlantic cod	17
Haddock		
Melanogrammus aeglefinus	Haddock	8
Demersal gadoids		
Gadus morhua	Atlantic cod	17
Melanogrammus aeglefinus	Haddock	8
Merlangius merlangus	Whiting	2
Pelagic gadoids		
Macruronus novaezelandiae	New Zealand hoki	3
Merluccius australis	New Zealand hake	3
Merluccius bilinearis	Silver hake	1
Pollachius virens	Pollock or saithe	1
Theragra chalcogramma	Walleye pollock	1
Ling		
Genypterus blacodes	New Zealand ling	4
Flatfish		
Hippoglossoides platessoides	American plaice	2
	Yellowtail flounder	6

data, we considered a gamma density curve and a logistic curve. For each of these curves, a scaling parameter was required, as the density under the gamma curve was not required to be 1, and the logistic curve was not necessarily asymptotic at 1. As the logistic model generally provided a better fit to the data, only the logistic model will be considered here.

Assuming lognormal observational errors, the three parameter logistic model for catchability-at-length $q(l)$, from data set i, has the form

$$(4) \qquad q_i(l) = \gamma_i' \frac{\exp(\alpha_i + \beta_i l)}{1 + \exp(\alpha_i + \beta_i l)} \exp(\varepsilon_{i,l})$$

where γ_i is the logarithm of maximum catchability, α_i and β_i are the traditional parameters describing the two-parameter logistic model, and $\varepsilon_{i,l} \sim N(0, \sigma_i^2)$. To constrain the estimates of γ_i' to be positive, we estimate $\gamma_i = \log(\gamma_i')$. This was also found to increase the speed of convergence and improve the mixing of the Bayesian model.

Modeling approaches

We used two distinct approaches in the modeling of catchability-at-length. Standard nonhierarchical modeling methods only utilize information from the data set in question, while hierarchical models have the ability to combine information from the data set with extra information from other independent data sets (Liermann and Hilborn 1997). Both approaches and their implementation will be discussed below.

Nonhierarchical models

Model I (individual data sets model)

In this case, we treat the parameters as fixed and survey specific for each data set. It is based on the unreasonable assumption that there is no relationship among estimates of catchability for the different surveys. This is the model shown in eq. 4. This model was fit using maximum likelihood rather than within a Bayesian framework. However, a Bayesian analysis with uninformative or reference priors should give the same results. Model I was run using the NLMINB function in S-Plus for each data set individually. The output from this model is the joint maximum likelihood estimates for the parameters of the logistic curve for each data set. These estimates were used to generate a logistic curve of catchability-at-length for each data set.

Hierarchical models

Hierarchical Bayesian modeling is one technique that allows the combination of data from independent sources (Gilks et al. 1994; Carlin and Louis 1996). When different data sets represent individual populations, such models assume that there is something in common about members of a taxonomic group and attempt to model that similarity in some way (Myers and Mertz 1998). Recently, the hierarchical Bayesian approach has enjoyed considerable popularity because it permits estimation of a very broad class of models and may produce more realistic assessments of the uncertainty of parameter estimates (Carlin and Louis 1996).

Bayesian estimation

Simply stated, the Bayesian estimation procedure combines information from two sources. The first is the statistical model of the data, $\mathbf{y}$, and the unknown parameter(s), θ, in the form of a probability distribution $f(\mathbf{y}|\theta)$. The second is the prior probability of the parameters $\pi(\theta|\eta)$, where η are the parameters of the prior distribution and are known as "hyper-parameters" (Carlin and Louis 1996). Bayesian inference is based on the posterior distribution $p(\theta|\mathbf{y},\eta)$ derived using Bayes Theorem:

$$p(\theta \mid \mathbf{y}, \eta) = \frac{f(\mathbf{y}|\theta)\pi(\theta \mid \eta)}{\int f(\mathbf{y}|\mathbf{u})\pi(\mathbf{u}|\eta)d\mathbf{u}}$$

This posterior distribution is used for Bayesian statistical inference as opposed to the frequentist approach, which uses $f(\mathbf{y}|\theta)$ for inference. When θ consists of a vector of unknown parameters, this posterior distribution represents the "joint" posterior distribution. By integrating out the other parameters, it is possible to obtain individual or "marginal" posterior distributions for each parameter of interest. In our case, the data $q_i(l)$ are model estimates of catchability-at-length from a species and survey.

Model II (random γ's, single α and β model)

This hierarchical model assumes a single α and β for all of the data sets within each meta-analysis groups but allows variation in the height parameter, γ_i. Thus, it is assumed that there is one single general shape for the logistic curve for catchability across the group, but the height of the curve varies across surveys. The estimates of the γ_i are assumed to come from a common distribution:

$$(5) \qquad q_i(l) = \gamma_i' \frac{\exp(\alpha + \beta l)}{1 + \exp(\alpha + \beta l)} \exp(\varepsilon_{i,l})$$

The hierarchical structure for γ_i is shown in Fig. 1. The γ_i's come from a normal prior distribution that is parameterized with a mean μ and variance σ^2 (the γ_i''s were lognormally distributed):

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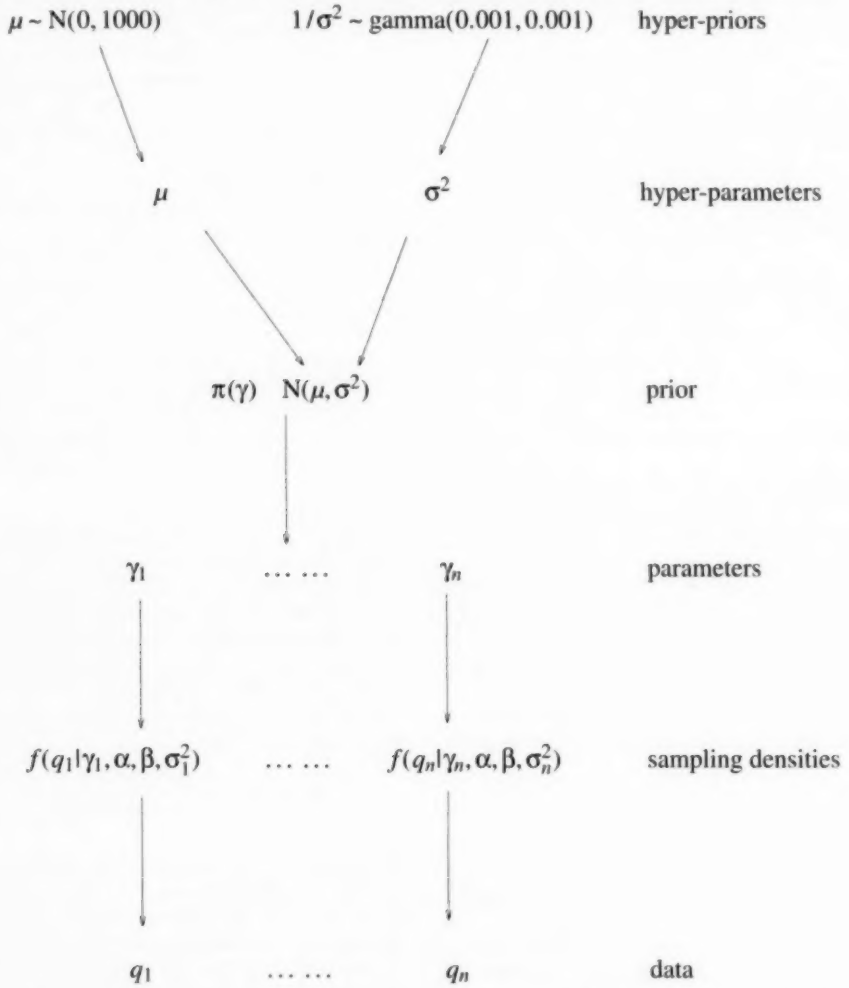
Fig. 1. General hierarchical structure of the model for the height of the logistic curve γ_i, $i = 1,\ldots,n$. The estimation error for the ith data set is given by σ_i^2, and σ^2 is the variance for the prior distribution for γ_i. (Following Efron 1996.)



$$\gamma_i \sim N(\mu, \sigma^2)$$

The parameters of these distributions are the hyper-parameters, which are also selected from their own prior (hyper-prior) distributions. A diffuse normal prior is used for the mean, μ (Fig. 1); this suggests that there is little prior information to suggest that any estimate of μ is a priori considered more probable than any other (note that this does imply that γ_i' is nonnegative). The conjugate prior for the variance of a normal distribution is the inverse gamma (Carlin and Louis 1996); here, we assume that the inverse of the variance, or precision, has prior probability given by a gamma distribution. Here, we parameterized the gamma distribution with two parameters (r, ω) such that

$$f(1/\sigma^2 | r, \omega) = \omega^r (1/\sigma^2)^{r-1} e^{-\omega(1/\sigma^2)} / \Gamma(r), \quad x > 0$$

where r is the "shape" parameter, ω is the inverse of the "scale" parameter, and $\Gamma(r)$ is the complete gamma function of r (Spiegelhalter et al. 1995). In the base case models, it was assumed that $1/\sigma^2 \sim \gamma(0.001, 0.001)$ (Fig. 1).

As opposed to the hierarchical structure of the estimates of γ_i, the parameters of the prior distributions for α and β were fixed rather than estimated. Very broad (almost flat) normal priors were assumed for α and β and the prior distributions were constrained using the upper and lower bounds (**I**(lower, upper)). These bounds are used to both constrain the parameters within very broad range of reasonable estimates and assist the Metropolis–Hastings algorithm. Another important consideration was the relative reliability of the different data sets. Here, we assumed that each data set had its own estimation error variance, σ_i^2, which was sampled from a known gamma distribution. Priors for these other parameters are

$$\beta_g \sim N(0.13, 10\,000)\mathbf{I}_{(0,0.5)}$$

$$\alpha_g \sim N(-5, 10\,000)\mathbf{I}_{(-20,-2.5)}$$

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$$\sigma_i^2 \sim \gamma(1\times10^{-6}, 1\times10^{-6})$$

Any possible influence of these constraints, and the hyperpriors, were assessed using alternative bounds and priors.

More complex models are possible in which all three parameters are assumed to come from their own common distribution. Such a model was not considered here due to the small numbers of data sets in each group.

For all groups except for ling, a seasonal categorical variable (summer–fall versus spring–winter) was added to help better model the difference in the mean maximum catchability μ within each group. In this case, we estimated a separate μ for each season (μ_s) but assumed that σ^2 was the same for each season. Thus, we allowed the mean of the distribution from which the γ_i's were drawn from to vary with season:

$$(6) \qquad \gamma_{i,s} \sim N(\mu_s, \sigma^2)$$

A Bayesian approach can be used to obtain estimates of individual parameters, e.g., mean or median of the marginal posterior distribution. It is the parameters derived from the marginal distributions that we will compare with the maximum likelihood estimates. In the process of calculating the joint posterior distribution, it is possible to calculate a value that is a function of the unknown parameters. This has the advantage of conserving any correlation structure that may exist between the unknown parameters. We used this approach to generate "predictive distributions" for catchability-at-length. If $q_{n+1}(\cdot)$ represents a new data set of observations of catchability-at-length, independent of the data used in the analysis, $\mathbf{q}(\cdot)$, given the underlying unknown parameters, θ, then the predictive distribution for $q_{n+1}(\cdot)$ is given by (after Carlin and Louis 1996)

$$(7) \qquad p(q_{n+1}(\cdot)\,|\,\mathbf{q}(\cdot)) = \int f(q_{n+1}(\cdot)|\theta)p(\theta|\,\mathbf{q}(\cdot))d\theta$$

where $\theta = (\sigma_i^2, \ldots, \sigma_n^2, \mu_s, \sigma^2, \alpha, \beta)$. This distribution summarizes all information concerning the new observations of catchability-at-length, given the likelihood, priors, and data observed (Carlin and Louis 1996).

The hierarchical Bayesian approach was implemented using BUGS (Bayesian Inference Using Gibbs Sampling) (Gilks et al. 1994). This is freely available software that can use both the Gibbs sampler and the Metropolis–Hastings algorithm to sample the joint posterior distribution for the parameters of interest. It is then possible to obtain estimates of the marginal posterior distributions for any function of the estimated parameters. This makes it possible to obtain estimates of uncertainty in the estimated parameters as well as to derive predictive distributions as functions of these estimated parameters, i.e., prediction of catchability-at-length as a function of the parameters of the scaled logistic.

Model runs

A hierarchical Bayesian analysis was conducted for each group and predictive intervals for length-specific catchability were determined. Model I was run using the NLMINB function in S-Plus for each data set individually and Model II was run for each of the meta-analysis groups described in Table 2 using BUGS. A "burn-in" of 5000 iterations was allowed, and following this, the Metropolis–Hastings algorithm was run for 200 000 iterations with every 100th sample retained. This reduced the autocorrelation in the chains. We retained 2000 samples of each parameter of interest (and functions thereof). Full BUGS model code for the models is available from the corresponding author.

Results

Maximum likelihood estimates were obtained from Model I for all data sets individually, and Bayesian estimates were obtained using Model II (Fig. 2). The Bayesian estimates from Model II were the median of the posterior distribution for the parameters of the scaled logistic, γ_i', α, and β. For some data sets, the maximum likelihood estimates were not sensible (e.g., Atlantic cod 4VsW, haddock 4TVsW, and pollock IV and IIIa). Also, for many of the Atlantic cod data sets, the data suggested very high catchability for the largest one or two sizes (e.g., 2J3KL fall, 3NO surveys, and IV and IIIa). However, it is likely that these were model artefacts.

The advantage of the Bayesian estimates in this situation is that they use information from other similar stocks to obtain improved estimates. In most cases where the maximum likelihood estimates were questionable, the Bayesian estimates appear to be far more reasonable. However, the Bayesian estimates for pollock and whiting were considerably different from the individual fits (Fig. 2). As the pollock and whiting data are from the North Sea surveys, there may be other factors leading to this difference (e.g., survey gear and substrate type) that are not being accounted for.

One motivation for using a Bayesian framework was the construction of predictive distributions for catchability-at-length. These could be used as auxiliary information for the analysis of a new data set for a group. The predictive distributions summarized by quantiles of the posterior distribution are given in Fig. 3 and Table 3. The uncertainty of these distributions reflects the variability between the stocks within each group. Separate distributions were generated for each season.

In the groups where season was modeled, catchability was higher for summer–fall surveys compared with those conducted in spring–winter. However, for the pelagic gadoid group, all but one of the surveys was from summer–fall. For the largest size-class modeled, catchability for summer–fall surveys for cod was about 20% higher, while for haddock, this difference was 60%.

For flatfish, catchability was also shown to be higher for the summer–fall surveys. Catchability-at-length was lower for flatfish than for any of the other groups. Catchability for Atlantic cod of a given length was less than that for haddock. Not surprisingly, catchability was higher for the demersal gadoids than for those that exhibit more pelagic behaviour. Catchability-at-length for ling was very low for small individuals but increased very rapidly between 60 and 80 cm. It is not certain what causes this dramatic increase, but it could be due to behavioural changes in adult ling.

Only in a very limited number of situations were the Bayesian estimates of catchability near to or higher than 1. Catchability of large haddock (>60 cm) for summer–fall surveys and catchability of large ling (>100 cm) were above 1. Maximum catchability of flatfish was below 0.5 for both seasons.

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Fig. 2. Individual maximum likelihood estimates for Model I (solid line), and Bayesian estimates based on the median of the marginal posterior for each the three parameters of the logistic curve Model II (dashed line) for each of the data sets used. Estimates for Atlantic cod and haddock are from the demersal gadoid model rather than the separate Atlantic cod and haddock analyses. (See Table 1 for details of each data set; the plots are in the same order.)

Robustness

One criticism of hierarchical Bayesian methods is the reliance on priors for the parameters describing the distribution of the random effects (hyper-priors). For sensitivity, we used $1/\sigma^2 \sim \gamma(1 \times 10^{-6}, 1 \times 10^{-6})$. This hyper-prior gives more weight to higher precisions and thus lower random effect variances. This sensitivity analysis was run for both demersal gadoids and flatfish. The results were almost identical, indicating the models were not sensitive to the choice of prior. While this is reassuring here, this result is not always the case when only a small number of data sets are available.

The upper and lower bounds for α and β were varied to test for sensitivity to the flat but bounded priors that were used. The results were insensitive to these changes.

Discussion

Estimation of the catchability of research trawl surveys is essential to both the management of single species and, more importantly, the reconstruction of fish communities and interpretation of their dynamics. Here, we have constructed length-specific catchability estimates for a number of species groups that will allow for increased understanding of fish community dynamics. First, we discuss our preference for hierarchical Bayesian analysis over more traditional fixed effects analysis. Second, we discuss the potential uses for the catchability estimates and the usefulness of this process as a potential diagnostic for stock assessments. Third, we compare our results with those of previous researchers. Finally, we consider the robustness of our results and discuss future extensions of our analysis.

Hierarchical modeling approach

In this analysis, we treat each survey/species combination as a random effect in a hierarchical model, as opposed to a more traditional fixed-effects model. This provides a more reliable estimator under a wide range of conditions (Robinson 1991). Also, in this approach, the estimates are consistent, while in the fixed-effect model, they are not. Kiefer and Wolfowitz (1956) noted that in estimation situations where the number of parameters increases to infinity, maximum likelihood parameter estimates are not consistent, but by treating parameters as coming from a distribution, i.e., as random effects, consistency could be obtained. Thus, if we assume that the suveys have something in common, then we can obtain better estimates than if we assume that the surveys are unrelated. This can clearly be seen by the comparison of the individual and Bayesian estimates of the catchability curves.

Because the same survey gear was not used for all surveys, this will lead to extra variability. This variability enters the model through the random effect variance (σ^2), which accounts for for all variability that cannot be accounted for by observation (or measurement) error alone. The use of separate means for the different seasons would act to reduce the random effect variance. The random effect approach does have an additional advantage over fixed effects for each survey gear, in that we can provide some estimates of catchability for a new survey gear type (for a given species) in the form of our predictive distributions.

Potential uses for estimates of length-specific catchability

Catchability estimates are generally only available for commercially important species that are formally assessed. Here, we estimate catchability for a number of species groups. As an application of the results of this study, a number of species from the Scotian Shelf were assigned to the different groups used in the meta-analysis. In this instance, length-specific catchability estimates have a considerable advantage over bulk estimates. For example, rather than assuming that the catchability of a red hake (*Urophycis chuss*) (size ≈ 50 cm) is the same as that of Atlantic cod (size ≈ 100 cm), we can assume that it has the same catchability as a 50-cm Atlantic cod. Full details of the assignment of catchability estimates to 78 fish species are given in Harley et al. (2001), a few examples of which will be discussed here.

Wolffish (*Anarhichas* sp.) and eelpout (*Lycodes* sp.) were assigned catchability estimates based on the ling analysis. New Zealand ling has an eel-like shape with no spiny fins or other means by which they can be easily caught in a trawl net. Grenadiers and sculpins were assigned to the demersal gadoid group. It may be useful to scale up estimates for sculpins because of the number of sharp spines that would lead to increased probabilities of retention in a trawl net.

For some species, length-specific catchability estimates were not considered appropriate. For sand lance (*Ammodytes* sp.) and capelin (*Mallotus villosus*), we recommended that a single estimate of catchability derived from the English groundfish survey for sand lance be used (from Sparholt 1990)). Edwards (1968) suggested that Barndoor skate (*Raja laevis*) showed escape behaviour that was different from that shown for flatfish and smaller skates. Thus, we recommend using Edwards' (1968) estimate rather than the length-specific estimate derived from the analysis of flatfish.

Hilborn and Liermann (1998) discussed the importance of the synthesis of existing information for the improved assessment of exploited fish populations. The results from a meta-analysis such as the one undertaken here could be incorporated into stock assessments in the form of auxiliary information. This could be done through Bayesian prior distributions (e.g., Punt and Hilborn 1997) or as a penalty function. For a stock assessment that estimates both survey selectivity and survey catchability (e.g., a common U.S. west coast assessment), it might be appropriate to set the maximum selectivity at 1 and then construct a prior distribution for catchability based on μ_s. This approach was used in the assessment of Pacific ocean perch off the coast of Washington and Oregon (Ianelli et al. 2000).

It is not clear how the results of a meta-analysis could be incorporated into a traditional VPA framework other than a diagnostic check on the VPA estimates. A less powerful way

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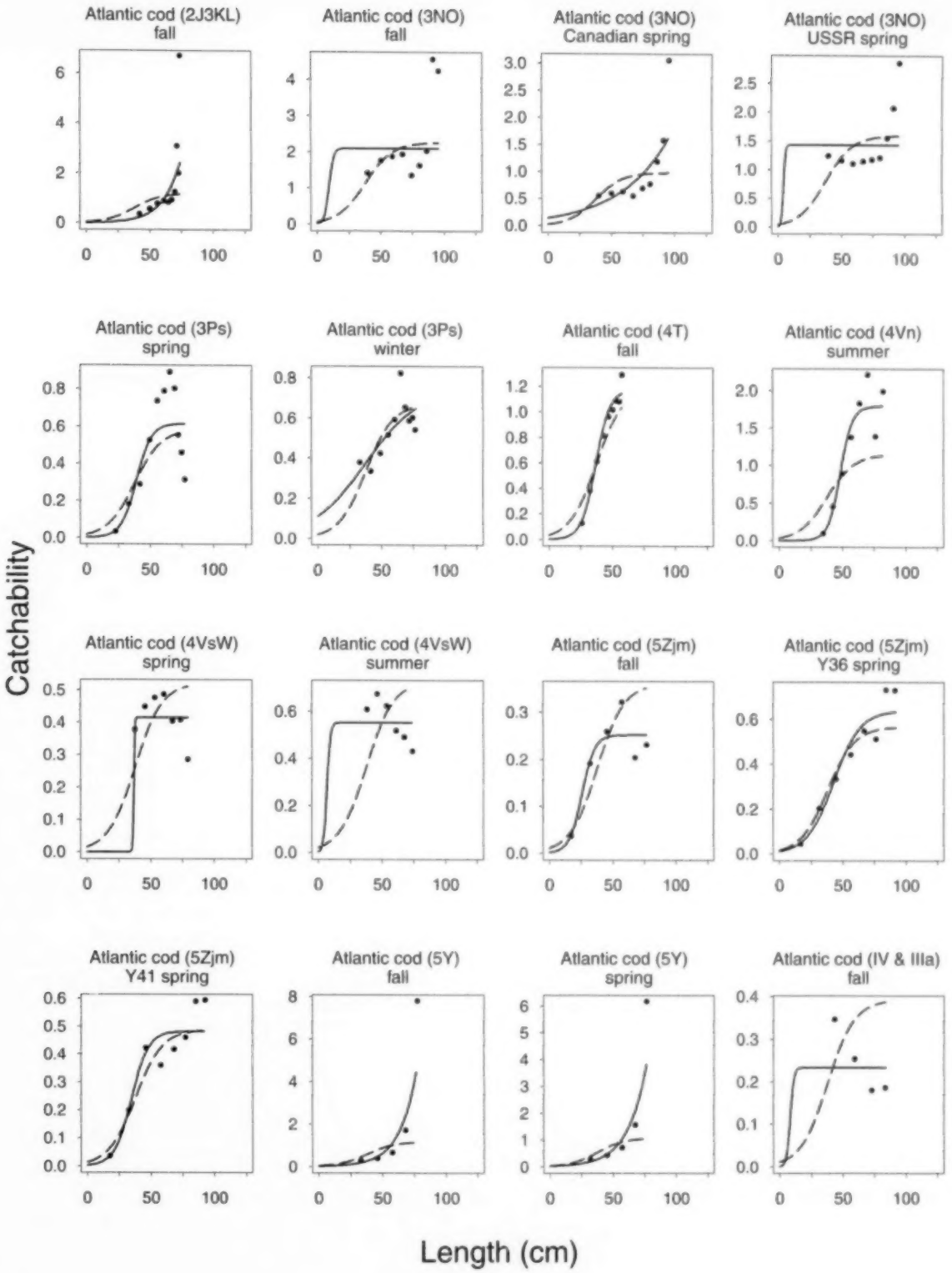
Atlantic cod (2J3KL) fall
Atlantic cod (3NO) fall
Atlantic cod (3NO) Canadian spring
Atlantic cod (3NO) USSR spring
Atlantic cod (3Ps) spring
Atlantic cod (3Ps) winter
Atlantic cod (4T) fall
Atlantic cod (4Vn) summer
Atlantic cod (4VsW) spring
Atlantic cod (4VsW) summer
Atlantic cod (5Zjm) fall
Atlantic cod (5Zjm) Y36 spring
Atlantic cod (5Zjm) Y41 spring
Atlantic cod (5Y) fall
Atlantic cod (5Y) spring
Atlantic cod (IV & IIIa) fall
Catchability
Length (cm)

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Fig. 2 (*continued*).

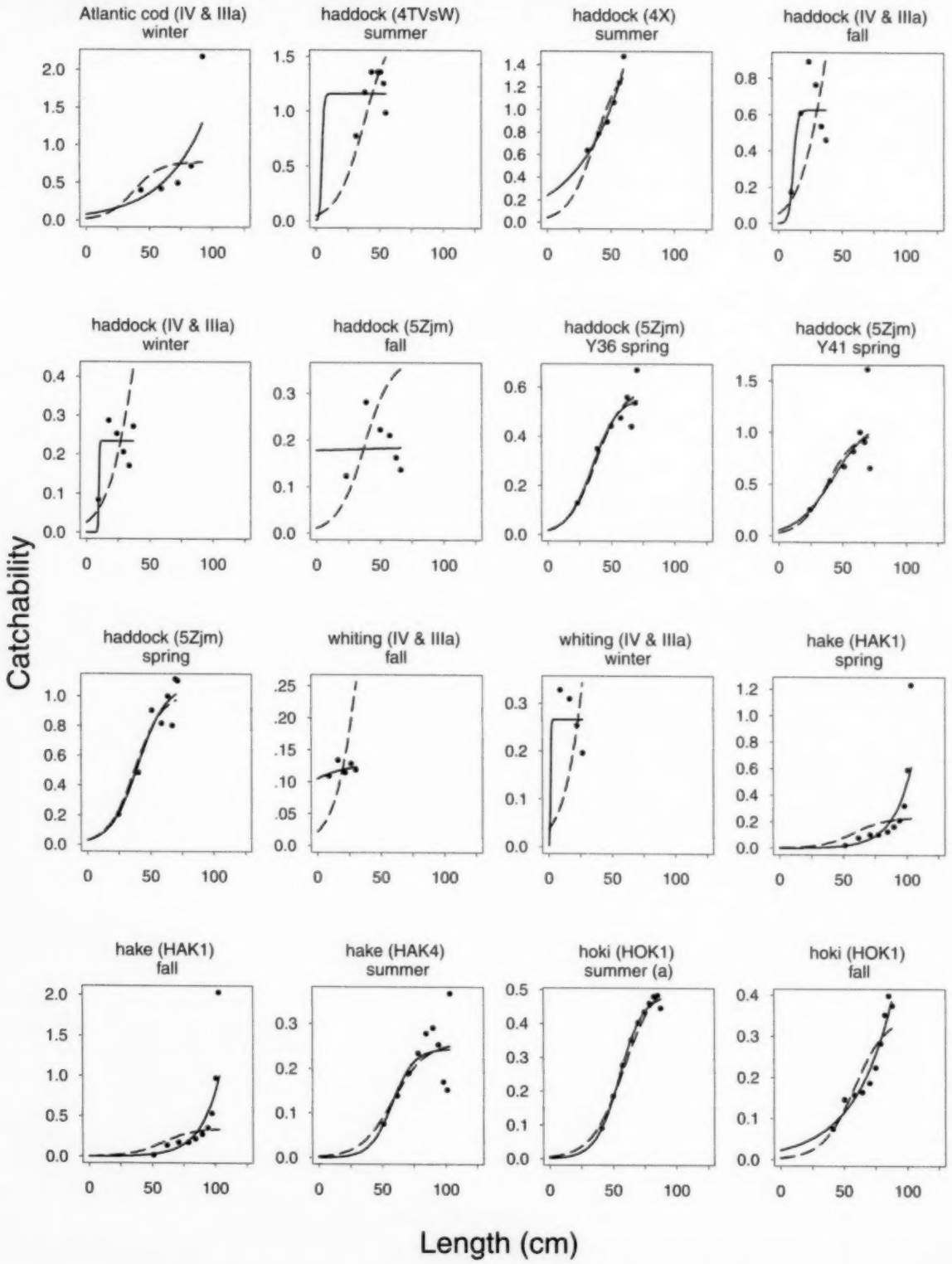

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Fig. 2 (*concluded*).

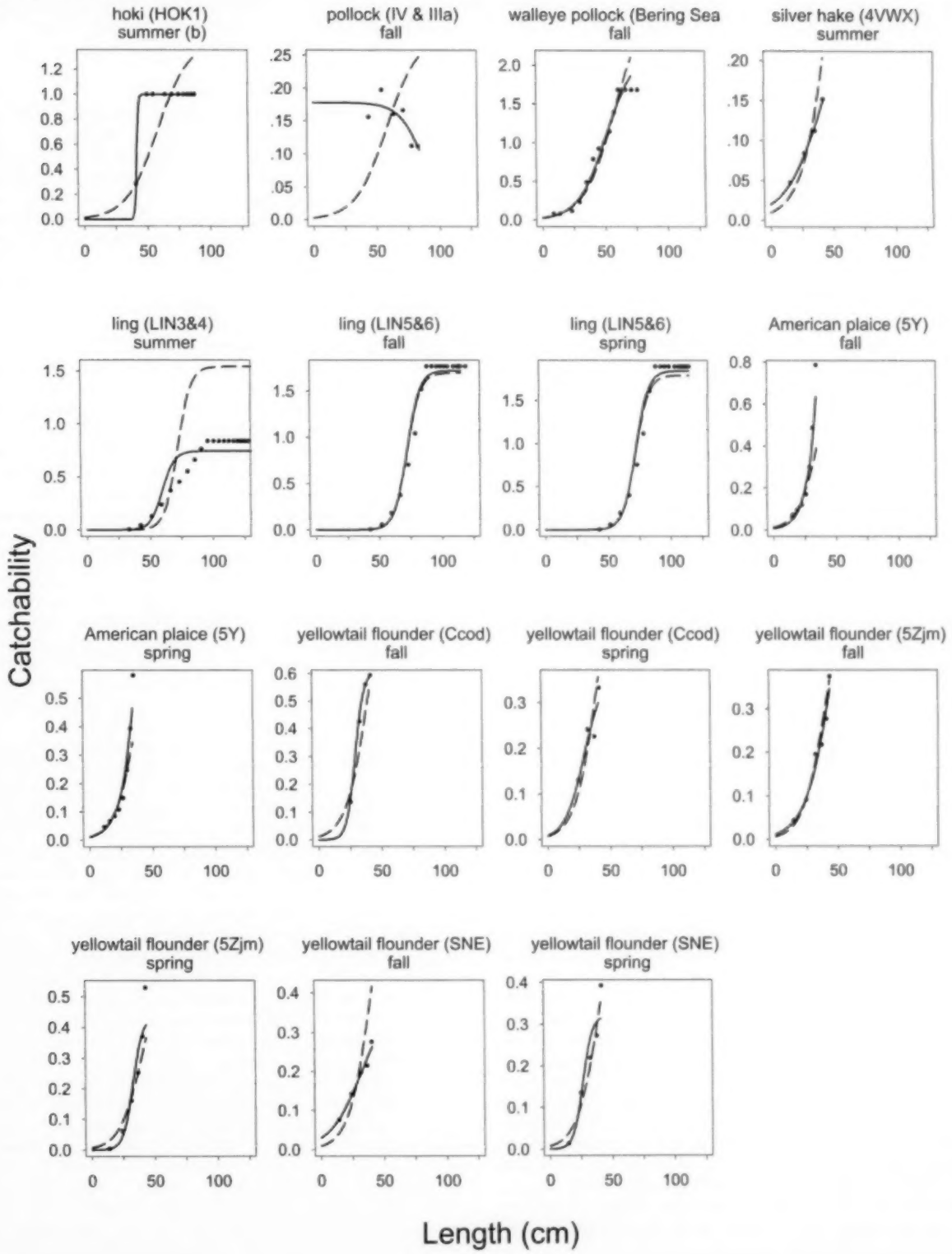

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Fig. 3. Predicted length-specific catchability for the different meta-analytical groups. Where a seasonal variable was included, estimates for both seasons are given. The solid line is the median of the posterior, the short-dashed lines are the 25th and 75th percentiles of the posterior predictive distribution, and the long-dashed lines are the 5th and 95th percentiles. The number of data sets used in each meta-analytic group is N,and n is the number of data sets for the particular season. The range of values of length correspond to that observed for the group.

to use these results would be by informally comparing stock assessment results with those from a meta-analysis. Another approach would be to conduct fully Bayesian assessments within a hierarchical framework. This would involve the simultaneous modeling of all of the populations and would involve some parameters (e.g., catchability or spawner–recruitment parameters) being estimated in a hierarchical manner. At present, this represents a daunting prospect in terms of both programming complexities and computational demands. However, if stock assessment science is to move forward, it is important that auxiliary information be able to be incorporated into stock assessment procedures.

In many assessments, survey indices are modeled as a mean catch rate rather than as area-swept abundance. In these circumstances, model estimates of "relative" catchability have no simple interpretation. Calculation of absolute catchability from catch rates is done using eq. 1 incorporating estimates of the area swept by a tow and the total survey area. Upon doing this calculation, we found that, for some data sets, estimates of catchability were greater than 4 (these data were excluded here). Very high estimates of catchability (i.e., greater than 2 or 3) imply that the survey catches considerably more than fish than would be predicted to be in the path of the tow (eqs. 2 and 3). Conversely, low estimates of catchability suggest that there are considerably more fish out there than are being caught by the survey. This could suggest that abundance is being overestimated by the model. We recommend that area-swept estimates of catchability be derived as a part of any stock assessment, as these values can be more easily interpreted and used as a diagnostic. In cases where catchability is either very high or low, this may suggest a problem with the assessment.

Comparisons with previous work

As this is the first study to estimate length-specific catchability estimates for a number of species, there are no other estimates that we can compare our results with. However, it is possible to make some comparisons with the bulk catchability estimates of Edwards (1968) and Sparholt (1990). Sparholt (1990) provided estimates for both the English Groundfish Survey (EGFS) and the International Young Fish Survey, but only the former will be discussed here. Both Edwards (1968) and Sparholt (1990) estimated haddock catchability to be higher than that of Atlantic cod, but both estimates are lower than that found here for larger individuals. Edwards' (1968) estimates for a given species were generally lower than that found by Sparholt (1990) except for flatfish where catchability for the EGFS was estimated at 0.096 compared with the range of 0.3–0.57 suggested for flatfish species by Edwards (1968). Our estimates for flatfish are more consistent with those of Edwards (1968). Overall, the qualitative conclusions regarding the relative catchability of various species are similar to those of previous researchers.

Although Atlantic cod and haddock share a number of morphological similarities, we have found that the catchability of haddock is higher than that of Atlantic cod. This implies behavioural differences in vertical availability to the trawl and (or) reaction to the trawl gear. Main and Sangster (1981) found that Atlantic cod and flatfish generally stayed low as the trawl passes, while haddock and whiting tend to swim upwards. This suggests that Atlantic cod are better at escaping under the ground gear of a bottom trawl than haddock are at escaping over the top.

Robustness and further work

A number of different sources of uncertainty have been included in our analysis, but there are additional sources of uncertainty that warrant consideration. First, we ignored variability in length-at-age by using a single von Bertalanffy growth function for each population. Second, we only allowed the height of the logistic curve to vary within each meta-analytic group. In doing so, we ignored any variability in α and β. However, this was necessary because of the small number of data sets that were in each group. Third, we assumed that any seasonal influences on catchability were the same for summer–fall and spring–winter surveys. Once again, small sample sizes imposed this restriction. Fourth, we assumed a functional form for the catchability curve that did not allow decreasing catchability at larger sizes. Finally, diel variability in catchability may result in differences between surveys conducted around the clock and those conducted during daylight hours only. These final two sources of uncertainty are discussed in greater detail below.

Thompson (1994) used a four-parameter logistic curve that allowed for a descending right-hand limb which in some cases may provide a better fit to the data than the three-parameter model assumed here. While there may be behavioural factors responsible for a descending right-hand limb in some cases, this descending limb is confounded (in estimation) with increased mortality at older ages (Thompson 1994). We believe that the logistic curve used here provides a good starting point but that curves allowing a descending right-hand limb should be considered in cases where observational studies support decreased catchability at larger sizes. It is possible to extend future analysis to include other models such as the four-parameter logistic curve used by Thompson (1994), but estimates from more complex models may be less reliable, as many data sets had only five to eight length/catchability observations.

Most research vessel surveys outside the Northwest Atlantic take place only during the daylight hours. While this appears to matter relatively little for some species, it makes a great deal of difference for others, e.g., sand lance (Casey and Myers 1998). As Casey and Myers (1998) found that the diel correction factor for Atlantic cod and haddock was not significantly different from 1, we have combined both day and day–night survey estimates for Atlantic cod, haddock, and the demersal gadoids. Although Casey and Myers

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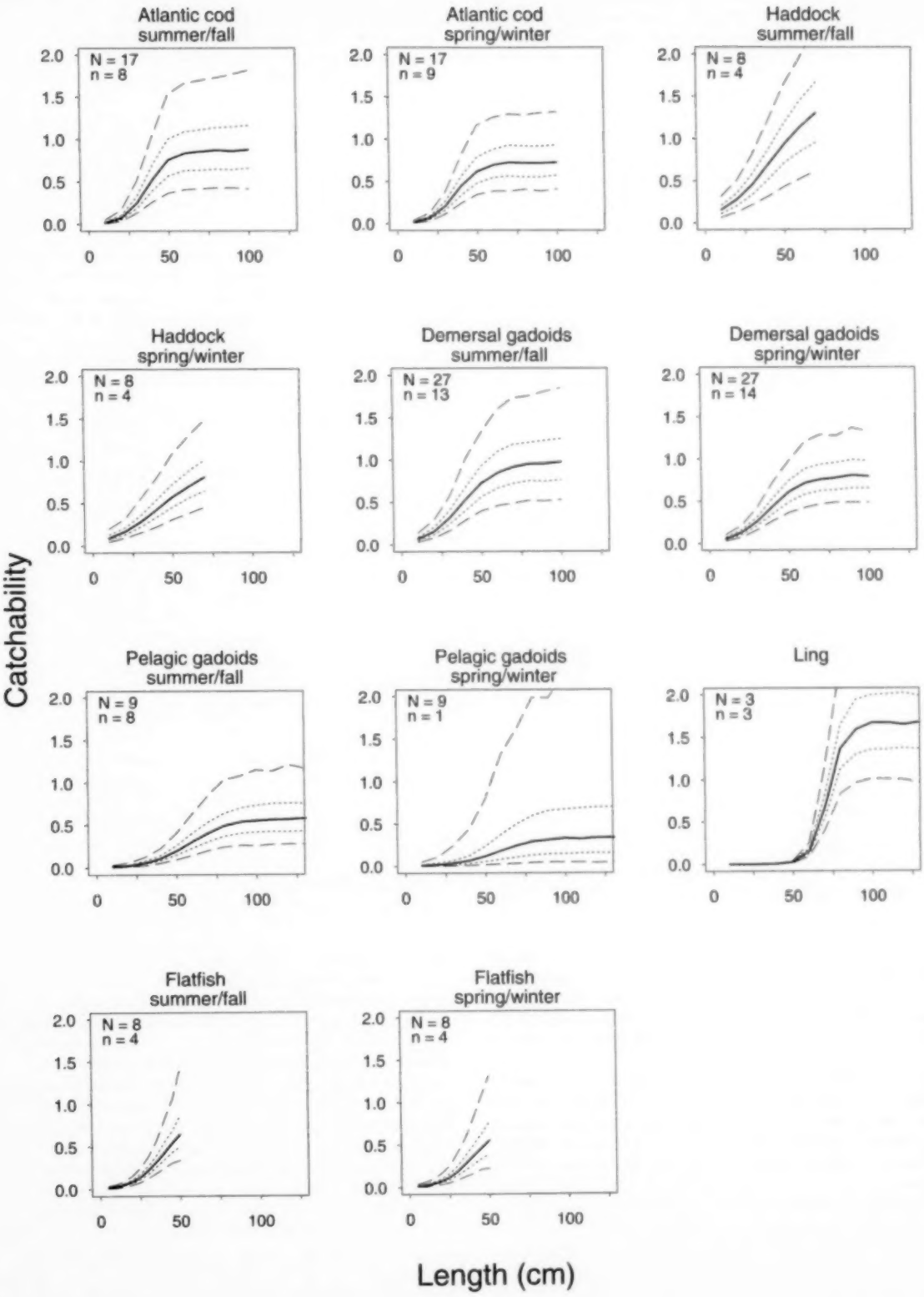

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Table 3. Parameters of the scaled logistic curve used to approximate the predictive distributions of catchability-at-length from Fig. 3.

	Summer–fall			Spring–winter		
	α	β	γ	α	β	γ
Atlantic cod						
$P_{0.05}$	–5.31	0.1490	0.422	–5.39	0.1470	0.396
$P_{0.25}$	–5.21	0.1440	0.651	–5.17	0.1410	0.562
$P_{0.5}$	–5.14	0.1410	0.870	–5.05	0.1380	0.719
$P_{0.75}$	–5.03	0.1380	1.150	–4.98	0.1360	0.917
$P_{0.95}$	–4.85	0.1310	1.760	–4.87	0.1330	1.310
Haddock						
$P_{0.05}$	–2.92	0.0707	0.679	–2.90	0.0688	0.507
$P_{0.25}$	–2.84	0.0694	1.080	–2.86	0.0684	0.736
$P_{0.5}$	–2.80	0.0661	1.500	–2.81	0.0663	0.931
$P_{0.75}$	–2.76	0.0628	1.990	–2.76	0.0645	1.180
$P_{0.95}$	–2.68	0.0588	2.860	–2.70	0.0633	1.740
$P_{0.05}$	–3.65	0.0969	0.522	–3.65	0.0981	0.484
$P_{0.25}$	–3.58	0.0943	0.758	–3.55	0.0950	0.650
$P_{0.5}$	–3.50	0.0925	0.968	–3.52	0.0938	0.797
$P_{0.75}$	–3.43	0.0908	1.240	–3.44	0.0908	0.988
$P_{0.95}$	–3.37	0.0871	1.830	–3.35	0.0868	1.350
Pelagic gadoids						
$P_{0.05}$	–4.70	0.0814	0.276	–4.67	0.0806	0.045
$P_{0.25}$	–4.63	0.0798	0.431	–4.62	0.0795	0.153
$P_{0.5}$	–4.61	0.0789	0.580	–4.58	0.0788	0.335
$P_{0.75}$	–4.57	0.0780	0.769	–4.59	0.0778	0.707
$P_{0.95}$	–4.53	0.0775	1.190	–4.60	0.0798	2.300
Flatfish						
$P_{0.05}$	–4.35	0.1240	0.398	–4.36	0.1190	0.275
$P_{0.25}$	–4.35	0.1160	0.609	–4.4	0.1170	0.485
$P_{0.5}$	–4.35	0.1110	0.831	–4.4	0.1120	0.716
$P_{0.75}$	–4.4	0.1060	1.190	–4.39	0.1070	1.060
$P_{0.95}$	–4.65	0.1020	2.220	–4.44	0.1010	2.010
Ling						
$P_{0.05}$	–13.80	0.1920	0.996			
$P_{0.25}$	–13.90	0.1930	1.360			
$P_{0.5}$	–13.90	0.1930	1.660			
$P_{0.75}$	–13.70	0.1900	2.010			
$P_{0.95}$	–13.60	0.1890	2.720			

Note: While the same α and β were assumed for each season, there are slight differences in the values, as these values are estimated by fitting to the quantiles of the samples from the predictive distributions.

(1998) provided diel corrections for many species on the Scotian Shelf, there are several important species, e.g., silver hake and pollock, for which diel corrections were not well estimated. When applying the meta-analytical estimates derived here to other species, it will be important to consider diel variability.

The seasonable variable used to model differences in the maximum catchability within a group suggested that trawl survey catchability is higher in summer–fall surveys than in spring–winter surveys. Due to the small number of data sets available, it is possible that season may be confounded with other factors or that the results are simply due to one or two extreme data sets. However, it is interesting that the same directional effect was observed for all four of the metaanalytic groups (not including the demersal gadoids, as the haddock and Atlantic cod data were considered separately). It is recommended that seasonal differences be investigated in more detail to attempt to confirm this finding and determine if this is also observed in other groups (e.g., herring and mackerel).

We considered Bayesian hierarchical models, which are only one of a family of hierarchical modeling techniques that could be used in this problem. The nonlinear mixed-effects model represents a frequentist approach that uses maximum likelihood type methods for the estimation of the parameters of the random effects distribution (Lindstrom and Bates 1990). Neither of these approaches is without its weaknesses. While Bayesian methods often rely heavily on prior specifications and require convergence of the Metropolis–Hastings algorithm to obtain accurate estimates of the posterior distributions, it is possible to estimate the random effect in mixed-effects models to be 0 (Searle et al. 1992). Further analyses will be performed to compare the performance of these approaches under different circumstances (i.e., the number of data sets and quality of the data in each group).

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Several extensions to our approach are possible, which would probably give improved results. We could model morphology and behaviour simultaneously in a meta-analysis, i.e., include species like ling with the demersal gadoids but include a parameter that describes the effects of morphology on catchability. It may also be possible to estimate gear effects and bottom type in more detail; however, we are primarily limited by data.

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Metabolic enzyme activity during smolting in stream- and hatchery-reared Atlantic salmon (*Salmo salar*)

Jill B.K. Leonard and Stephen D. McCormick

Abstract: To evaluate the metabolic differences between Atlantic salmon (*Salmo salar*) parr and smolts and the effect of rearing environment, we examined metabolic enzyme activity in white muscle, liver, and heart in stream- and hatchery-reared juveniles. Spring increases in gill Na^+,K^+-ATPase (3.5-fold) and cardiosomatic index (37–69%) and decreases in condition factor (~17%) occurred in smolts, but not in parr. White muscle phosphofructokinase (PFK) increased during spring and was 3.6-fold higher in smolts than in parr by late spring. There were seasonal increases in liver citrate synthase (CS) (~42%), liver β-hydroxyacyl-coenzyme A dehydrogenase (HOAD) (~60%), and heart CS (~23%) and decreases in liver lactate dehydrogenase (LDH) (~28%) in parr and smolts. Activity of liver HOAD was greater in stream-reared smolts (~18%) than in parr or hatchery smolts. Heart PFK activity increased during spring in wild-reared parr and smolts, while it decreased in hatchery-reared smolts. White muscle LDH and PFK increased earlier in spring in hatchery- than in stream-reared smolts. Our results suggest that increased heart size and high white muscle PFK occur during smolting and may be adaptive for downstream and ocean migration. Hatchery- and stream-reared Atlantic salmon differ in the timing of metabolic changes during smolting, which may impact their long-term survival.

Résumé : Un examen de l'activité des enzymes métaboliques du muscle blanc, du foie et du coeur chez des jeunes Saumons de l'Atlantique (*Salmo salar*) élevés en ruisseau et en pisciculture a été entrepris pour évaluer les différences métaboliques entre les tacons et les saumoneaux et les effets du milieu d'élevage. Au printemps, la Na^+,K^+-ATPase des branchies augmente de 3,5 fois et l'indice cardiosomatique de 37–69%, alors que le coefficient d'embonpoint diminue (~17%) chez les saumoneaux, mais pas chez les tacons. La phosphofructokinase (PFK) du muscle blanc augmente au printemps et elle est 3,6 fois plus élevée chez les saumoneaux que chez les tacons à la fin du printemps. Il y a des augmentations saisonnières de la citrate synthase (CS) du foie (~42%) et du coeur (~23%) et de la β-hydoxyacyl-coenzyme A déshydrogénase (HOAD) du foie (~60%) chez les tacons et les saumoneaux, ainsi qu'une diminution de la lactate déshydrogénase (LDH) du foie (~28%). L'activité de la HOAD du foie est plus grande (~18%) chez les saumoneaux de ruisseau que chez les tacons ou les saumoneaux de pisciculture. L'activité de la PFK du coeur augmente au cours du printemps chez les tacons et les saumoneaux sauvages, mais elle diminue chez les saumoneaux de pisciculture. La LDH et la PFK du muscle blanc augmentent plus tôt chez les saumoneaux de pisciculture que chez les saumoneaux de ruisseau. Nos résultats indiquent que, durant la saumonification, la taille du coeur s'accroît et la PFK augmente dans le muscle blanc, ce qui pourrait être des adaptations pour la migration vers l'aval et l'océan. Les Saumons de l'Atlantique élevés en pisciculture et en ruisseau diffèrent dans la phénologie de leurs changements métaboliques durant la saumonification, ce qui peut affecter leur survie à long terme.

[Traduit par la Rédaction]

Introduction

Alteration of metabolism during the parr–smolt transformation has been found in several salmonid species. In Atlantic salmon (*Salmo salar*), standard and active metabolic rates are 50% higher in smolts than in parr (Maxime et al. 1989). Maxime et al. (1989) suggested that this elevation of metabolic rate in smolts might be due to elevated respiratory enzyme activity and mitochondrial proliferation resulting from an increase in thyroid hormone levels. Metabolism may also increase due to the metabolic demands of development and differentiation (McCormick and Saunders 1987). Atlantic salmon smolts have decreased available liver and muscle glycogen compared with parr (Fontaine and Hatey 1953;

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Wendt and Saunders 1973) as well as elevated levels of blood glucose (Wendt and Saunders 1973). In coho salmon (*Oncorhynchus kisutch*) smolts, decreased glycogen is caused by a combination of decreased glycogen synthesis and increased glycogenolysis in the liver (Sheridan et al. 1985). Lipid metabolism is also altered during the parr–smolt transformation such that total body and muscle lipid decreases in smolts (Saunders and Henderson 1970, 1978). Evidence from chinook (*Oncorhynchus tshawytscha*) (Cowley et al. 1994) and coho salmon (Sheridan et al. 1985; Sheridan 1986) indicates that lipid depletion is caused by increased lipolysis and decreased fatty acid synthesis. There is also some evidence that there is a reorganization of amino acid distribution during smoltification; however, there was no net change in the total amino acid content of smolts (Fontaine and Marchelidon 1971). It has been suggested that this reorganization is linked to guanine and hypoxanthine deposition in the skin and scales (smolt silvering, Fontaine and Marchelidon 1971) as well as possible changes in cellular osmoregulatory gradients (McCormick and Saunders 1987). There is also evidence that there is an elevation of activity of respiratory enzymes in the gill (Chernitsky and Shterman 1981; Langdon and Thorpe 1985; McCormick and Saunders 1987) and liver (Blake et al. 1984) of Atlantic salmon smolts.

The work described above concentrated on laboratory studies using hatchery-reared fish as experimental animals. While it is likely that these changes also occur in the wild, it is unknown if there are substantial differences in smolt-associated metabolic changes between hatchery-reared and stream-reared salmon. Possible differences in smolt development due to rearing environment are of particular interest due to the usually poor return rates of hatchery fish compared with wild fish (briefly reviewed by McCormick et al. 1998). Recently, there has also been an increased use of fry rather than smolt releases to restore depleted salmonid stocks (e.g., Rideout and Stolte 1988), and there is little knowledge of smolt development in salmonids released as fry.

Evidence suggests that there are substantial differences in development that occur between salmon reared in the hatchery environment and salmon reared in the wild. Brauner et al. (1994) demonstrated an effect of rearing environment on the swimming ability of coho salmon smolts. McDonald et al. (1998) also showed an effect of rearing habitat on swimming capacity in Atlantic salmon juveniles that was difficult to overcome even in modified hatchery rearing environments. Shrimpton and co-workers found significant differences in cortisol dynamics, including receptor level differences and circulating hormone concentrations, between stream- and hatchery-reared coho salmon smolts (Shrimpton et al. 1994*a*, 1994*b*), while McCormick and Bjornsson (1994) found differences in thyroid hormone and growth hormone profiles between hatchery- and wild- reared Atlantic salmon juveniles.

We are interested in further examining the physiological differences between fish that undergo smoltification in the wild and those that smolt in a hatchery environment in an effort to understand the underlying basis for potential differences in survival of smolts reared in hatcheries and in the wild. In this study, we focus on differences in the capacity of metabolic enzymes between parr and smolts (as determined by Na^+,K^+ ATPase activity) and the impact of rearing environment on these developmental changes. Specifically, we have focused on several enzymes critical to glycolysis (phosphofructokinase (PFK)), fatty acid metabolism (β-hydroxyacyl-coenzyme A dehydrogenase (HOAD)), aerobic metabolism (citrate synthase (CS)), and lactate regulation (lactate dehydrogenase (LDH)).

Materials and methods

Fish

Stream-reared Atlantic salmon were collected by electrofishing in West Salmon Brook, Connecticut, on March 15 (3.0°C), April 5 (5.0°C), and June 2 (14.5°C, parr only), 1994. There is no natural reproduction above any mainstem dam in the Connecticut River, and since all smolt releases occur in the mainstem of the river, stream-reared fish were easily identified. Migrating stream-reared smolts were captured at downstream bypass structures at hydroelectric facilities on the Farmington River (15 km downstream of West Salmon Brook) on May 20 and 25 and at Cabot Station on the Connecticut River on May 11 and 20. The size distributions in March and April showed a clear distinction between 1-year-old parr and 2-year-old smolts. One-year-old fish from the White River National Fish Hatchery (Bethel, Vt.) were sampled on March 21 (2.8°C), April 6 (3.0°C), and May 11 (11.9°C). Those captured on May 11 had been released from the hatchery on April 14 and subsequently captured at Cabot Station and thus were active migrants. Hatchery-reared smolts were easily distinguished because all fish released from the hatchery as smolts are adipose fin clipped. Due to the natural temperature changes occurring over the period of the study, fish could not be sampled at the same temperature. While this has the potential to confound our results, it was unavoidable in a field-based study. It should be emphasized that seasonal effects found in this study may well include the effect of temperature on the juvenile salmon, along with other seasonally linked parameters such as photoperiod or increasing wild food availability; however, since all groups were experiencing similar temperatures over the period of sampling, rearing effects (between groups) are unlikely to be a function of temperature per se.

Sampling

Captured fish were anaesthetized with 100 $mg \cdot L^{-1}$ tricaine methansulfonate (MS-222, pH 7.0). Fish were measured for mass and fork length and then bled from the caudal vessels. The heart was removed by cutting posterior to the bulbus arteriosus and anterior to the sinus venosus. The heart was then blotted dry to remove internal blood, weighed, and frozen immediately on dry ice. The liver was also removed, weighed, and frozen. A sample of white muscle was excised from the left side of the fish dorsal to the midline, anterior to the dorsal fin, weighed, and frozen. A gill biopsy was taken from the second gill arch. Approximately three to five gill filaments were cut above the septa and placed in 100 µL of SEI buffer (150 mM sucrose, 10 mM EDTA, 50 mM imidazole, pH 7.3) and frozen. All samples were then returned to the laboratory where they were stored at –80°C for later assay.

Enzyme assays

We measured four metabolic enzymes in heart, liver, and white muscle: CS (Guderley et al. 1986; McCormick et al. 1989), HOAD (Bradshaw and Noyes 1975; Guderley and Gawlicka 1992), PFK (Ling et al. 1966; Guderley and Gawlicka 1992), and LDH (Vassault 1983; Guderley and Gawlicka 1992). Samples were homogenized in a buffer containing 50 mM imidazole, 2 mM EDTA, 5 mM $MgCl_2$, and 1 mM glutathione at pH 7.5. Tissues were homogenized using a ground glass homogenizer in 20 volumes of ice-cold homogenization buffer. Homogenates were then centri-

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fuged at 3000 × *g* for 5 min and the supernatant was immediately assayed kinetically at 25°C in 96-well microplates using the following specific conditions.

CS (EC 4.1.3.7): 50mM Tris, 0.78 mM 5,5′-dithiobis-(2-nitrobenzoic acid), 0.17 mM acetyl coenzyme A, 0.57 mM oxaloacetic acid (omitted for control), pH 8.1. Read at 412 nm.

PFK (EC 2.7.1.1): 75 mM Tris–HCl, 200 mM KCl, 6 mM $MgCl_2$, 1 mM KCN, 2 mM AMP, 1.75 mM ATP, 0.16 mM NADH, 4 units of triose phosphate isomerase, 4 units of 3-phosphoglycerol dehydrogenase, 4 units of aldolase, 5 mM fructose-6-phosphate (omited for control), pH 8.0. Read at 340 nm.

LDH (EC 1.1.1.27): 100 mM potassium phosphate, 0.4 mM pyruvate, 0.16 mM NADH, pH 7.0. Read at 340 nm. This assay was routinely run without control, since preliminary experiments showed extremely low activity (<2% of total) in the absence of substrate (pyruvate) in all tissues.

HOAD (EC 1.1.1.35): 100 mM triethanolamine HCl, 5 mM EDTA, 1 mM KCN, 0.23 NADH, 0.15 acetoacetyl coenzyme A (omitted for control), pH 7.0. Read at 340 nm.

All metabolic enzyme assays were run in duplicate and the activities expressed in international units (i.e., micromoles of substrate transformed to product per minute per gram wet mass tissue.

Gill Na^+,K^+-ATPase (EC 3.6.1.3): Na^+,K^+-ATPase activity was determined with a kinetic assay run in 96-well microplates at 25°C and read at a wavelength of 340 nm for 10 min (McCormick 1994). Gill tissue was homogenized in 125 µL of SEID (SEI buffer and 0.1% deoxycholic acid) and centrifuged at 5000 × *g* for 30 s. Ten-microlitre samples were run in two sets of duplicates: one set containing assay mixture and the other assay mixture and 0.5 mM ouabain. The resulting ouabain-sensitive ATPase activity is expressed as micromoles of ADP per milligram of protein per hour. Protein concentrations were determined using the BCA (bicinchoninic acid) protein assay (Pierce, Rockford, Ill.).

Statistics and calculations

Cardiosomatic index (CSI) was calculated as (heart mass·total mass $^{-1}$) × 100. Hepatosomatic index (HSI) was calculated as (liver mass·total mass $^{-1}$) × 100. Condition factor was calculated as (total mass·length^{-3}) × 100. Length, weight, CSI, HSI, Na^+,K^+-ATPase, and condition factor data were analyzed using analysis of variance (ANOVA) and analysis of covariance (ANCOVA) with length as a cofactor. All metabolic enzyme data were also analyzed using multivariate analysis of variance (MANOVA) followed by post hoc testing using ANOVA. Further post hoc testing of all ANOVA results used the least square means general linear models procedure after testing for the appropriate statistical assumptions using SAS (SAS Institute Inc., Cary, N.C.) for each significant factor.

Results

There was no significant difference in gill Na^+,K^+-ATPase levels (*t* test, $p = 0.55$) between stream-reared smolts captured in the Farmington and Connecticut rivers, suggesting that these fish were at similar smolt and migratory stages. As a result, data for all stream-reared smolts were pooled and comparisons presented are between parr, stream-reared smolts, and hatchery-reared smolts at three time periods. At all sampling times, hatchery smolts were always longer and heavier than stream-reared smolts and all smolts were larger than parr ($p = 0.001$). Parr and stream-reared smolts were significantly longer (ANOVA, $p = 0.001$) in May (note: data from June sampling are included in this group) than in March (Fig. 1*a*), whereas hatchery smolts were not significantly longer at the end of the study. There was no significant increase in weight over the course of the study within any of the groups when all groups were analyzed together ($p = 0.11$) (Fig. 1*c*). Parr were significantly larger in May when ANOVA was performed on parr data alone ($p = 0.001$). Condition factor differed between the groups and over time ($p = 0.001$); condition factor of parr increased over the course of the study, while smolts had decreased condition factor in May (Fig. 1*b*).

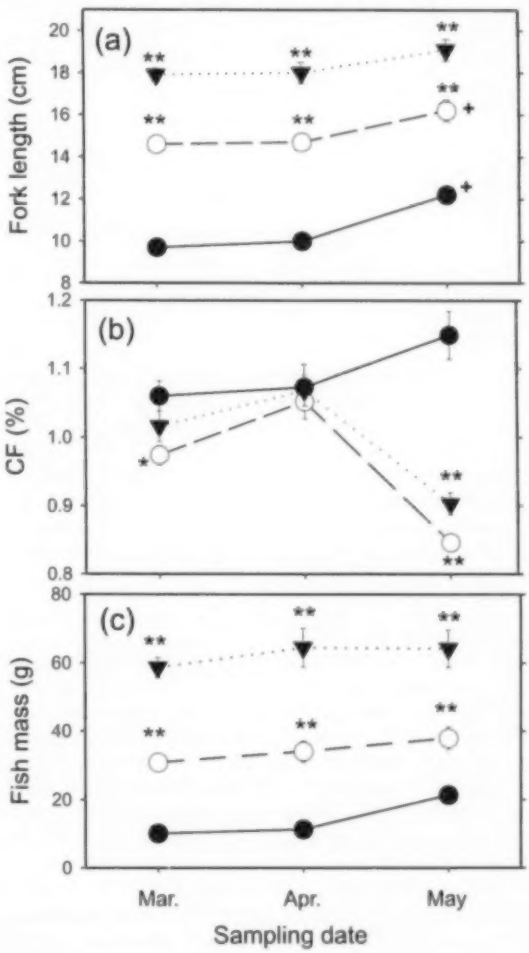

Fig. 1. (*a*) Fork length, (*b*) condition factor, and (*c*) fish mass of Atlantic salmon parr (●), stream-reared smolts (○), and hatchery-reared smolts (▼) sampled during March, April, and May–June 1994 in the Connecticut River watershed. Data are means ± SE. A plus sign indicates a significant increase in length within a juvenile salmon group over March values. A single asterisk indicates a significant difference from parr activity at a given sampling time and a double asterisk indicates a significant difference from the other two juvenile salmon groups at a given sampling time. Statistics indicate ANOVA and post hoc testing with $\alpha = 0.05$.

Gill

Gill Na^+,K^+-ATPase activity was below 4 µmol·mg protein^{-1}·h^{-1} in all groups during March and April. In May, both

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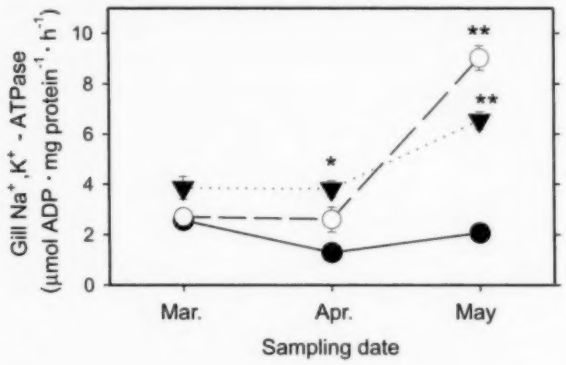
Fig. 2. Gill Na^+,K^+-ATPase of Atlantic salmon parr (●), stream-reared smolts (○), and hatchery-reared smolts (▼) sampled during March, April, and May–June 1994 in the Connecticut River watershed. Data are means ± SE. A single asterisk indicates a significant difference from parr activity at a given sampling time and a double asterisk indicates a significant difference from the other two juvenile salmon groups at a given sampling time. Statistics indicate ANOVA and post hoc testing with $\alpha = 0.05$.



stream- and hatchery-reared smolts showed significantly elevated Na^+,K^+-ATPase activity, with stream-reared smolts showing the greatest elevation (3.5-fold) over earlier levels (Fig. 2). There was no change in gill Na^+,K^+-ATPase of parr in May. Na^+,K^+-ATPase was not significantly affected by fish length. During May, all groups were significantly different from one another, with Na^+,K^+-ATPase of hatchery- and stream-reared smolts being 3.2-fold and 4.3-fold higher, respectively, than that of parr.

Metabolic enzymes

The overall MANOVA showed significant effects of fish stages ($p < 0.001$), sampling date ($p < 0.001$), and the interaction between these factors ($p < 0.001$) on combined metabolic activity (all enzymes in all tissues). We will further describe these results in more detail, incorporating results of tissue- and enzyme-specific ANOVA. There was no affect of length on any of the following parameters as adjudged by ANOVA with length as a covariate.

Heart

CSI remained constant in parr but increased significantly in smolts in May (Fig. 3*a*). CSI in May was significantly different in all groups and was elevated by 37 and 69% for hatchery- and stream-reared smolts, respectively, over parr values.

Heart CS increased in activity over the course of the study in all groups by approximately 23% (MANOVA, $p < 0.001$), and there was a marginally significant difference between the groups ($p = 0.052$) (Fig. 3*c*). There was a significant interaction (ANOVA, $p = 0.03$) between sampling time and group, which was a result of a slightly lower CS activity in hatchery smolts in May.

Heart HOAD differed between the groups of juvenile salmon (MANOVA, $p = 0.009$), but did not differ between sampling times ($p = 0.39$) (Fig. 3*d*).

Heart LDH did not change significantly during the study (MANOVA, $p = 0.44$), nor did the three groups vary significantly ($p = 0.86$). There was a significant interaction between group and sampling date ($p = 0.003$) resulting from a tendency for stream-reared smolts to have decreased activity in April, while hatchery smolts tended to have slightly higher activity (Table 1).

Heart PFK differed significantly with sampling time (MANOVA, $p = 0.03$) and there was a significant interaction between time and group (ANOVA, $p = 0.001$), although MANOVA showed no significant difference between juvenile groups ($p = 0.77$). In March, heart PFK of hatchery smolts was elevated over that of both parr and stream-reared smolts (Fig. 3*b*). In April, hatchery smolt heart PFK did not significantly differ from that of the other groups. In May, PFK levels of both parr and stream-reared smolts were elevated over initial levels and were significantly higher than those of hatchery smolts.

Liver

HSI differed significantly (ANOVA, $p = 0.0001$) (Fig. 4*a*) between the groups of juvenile salmon, and although there was no significant difference between sampling times ($p = 0.41$), there was a significant interaction between group and sampling time ($p < 0.01$). On average, hatchery smolt HSI was 35% higher than that of parr, while there was no difference between parr and stream-reared smolts. The interaction is an indication of a tendency for hatchery smolts to have a slightly elevated HSI in the early sampling times, while stream-reared smolts and parr tended to increase HSI slightly over time.

Liver CS differed significantly between groups (MANOVA, $p < 0.001$) and sampling times ($p < 0.001$). Stream-reared smolts had consistently higher liver CS activities (~13% higher than parr) than the other groups (Fig. 4*c*). All three groups had increased liver CS activity over the course of the study (~42%).

Similar to liver CS, liver HOAD showed a pattern of increased activity with time (~60%; $p < 0.001$) (Fig. 4*d*). Stream-reared smolts had a significantly higher enzyme activity level (18% higher than parr) than the other two groups ($p = 0.001$).

Liver LDH (Fig. 4*b*) differed significantly with sampling date (MANOVA, $p < 0.001$) and juvenile group ($p < 0.001$), and there was a significant interaction between sampling date and group (ANOVA, $p = 0.001$). Liver LDH activity of hatchery- and stream-reared smolts decreased progressively from March to May. Liver LDH activity of parr decreased from March to April, but then increased in May and was almost double that of smolts in May.

Liver PFK did not differ significantly with sampling date (MANOVA, $p = 0.52$) or juvenile salmon group ($p = 0.88$) (Table 1). There was a slight, but significant, interaction between sampling date and group (ANOVA, $p = 0.02$).

White muscle

White muscle CS differed significantly between groups (MANOVA, $p < 0.001$) and sampling dates ($p = 0.01$), and there was a significant interaction between sampling date and group (ANOVA, $p = 0.03$). There was no significant difference in white muscle CS activity in hatchery smolts over

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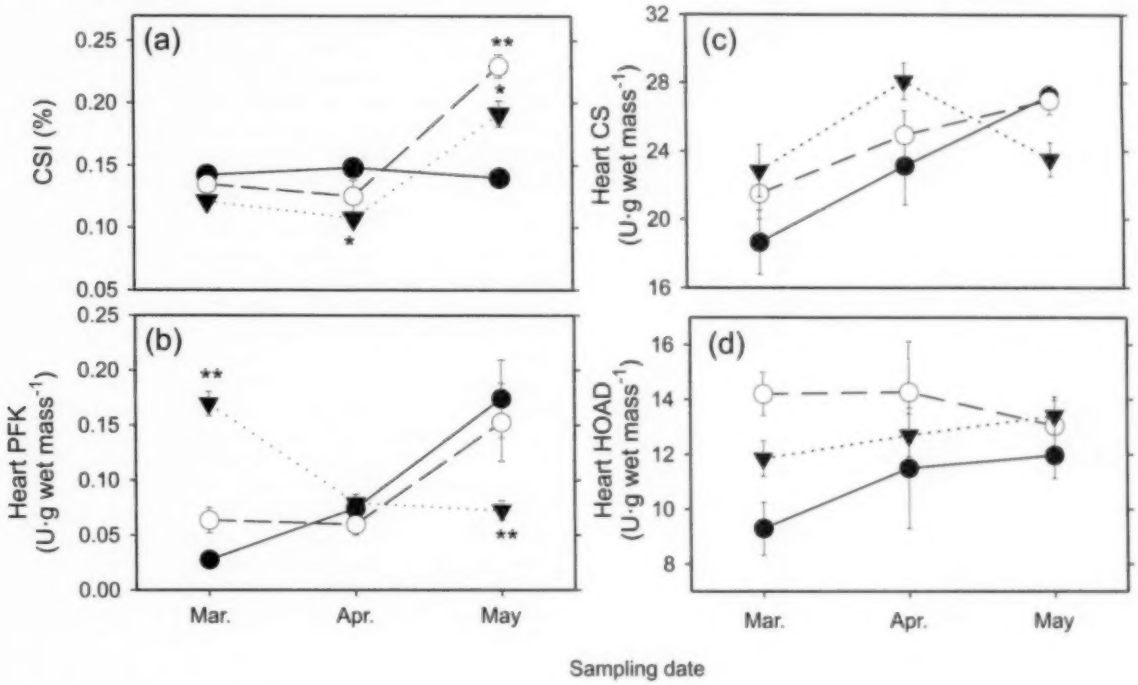
Fig. 3. (*a*) CSI, (*b*) heart PFK activity, (*c*) heart CS activity, and (*d*) heart HOAD activity of Atlantic salmon parr (●), stream-reared smolts (○), and hatchery-reared smolts (▼) sampled during March, April, and May–June 1994 in the Connecticut River watershed. Data are means ± SE. A single asterisk indicates a significant difference from parr activity at a given sampling time and a double asterisk indicates a significant difference from the other two juvenile salmon groups at a given sampling time. Statistics indicate ANOVA and post hoc testing with $\alpha = 0.05$.



the course of the study (Fig. 5*b*). In contrast, both parr and stream-reared smolts had elevated white muscle CS early in the study followed by lower levels in May. Parr showed the greatest decrease in activity (–43%) between April and May.

White muscle HOAD did not change significantly during the study (MANOVA, $p = 0.31$) (Table 1), nor were the juvenile salmon groups significantly different ($p = 0.56$).

White muscle LDH significantly differed between sampling dates (MANOVA, $p < 0.001$) and groups ($p < 0.001$), and there was a significant interaction between sampling date and group (ANOVA, $p = 0.001$). LDH activity in hatchery smolts was significantly higher ($p = 0.001$) in April than in March or May (Fig. 5*c*). Both parr and stream-reared smolts had low LDH activity in March and April but had significantly higher LDH activities in May (85 and 56% increases, respectively; $p = 0.001$).

White muscle PFK differed significantly between sampling dates (MANOVA, $p = 0.001$) and juvenile groups ($p < 0.001$), and there was a significant interaction between sampling date and group (ANOVA, $p < 0.001$). Parr white muscle PFK did not change significantly over the course of the study when analyzed using ANOVA that included smolt data; however, when the parr were analyzed separately from the smolts, there was a significant increase in activity in May over earlier levels ($p = 0.001$) (Fig. 5*a*). Both groups of smolts showed increased white muscle PFK during the study; hatchery-reared smolt white muscle PFK was highest in April (2.7-fold increase), while stream-reared smolt PFK was highest in May (3.6-fold increase).

Discussion

The large increases in gill Na^+,K^+-ATPase activity and decreases in condition factor in hatchery- and stream-reared smolts indicate that these fish, which were selected as putative smolts based on their size and appearance, were indeed smolting in the spring. Smolts captured in May–June were active migrants, which further supports their classification as smolt-stage juveniles. Increased gill Na^+,K^+-ATPase activity is frequently used as an indicator of smolting in salmonids and results from the increased number of mitochondrial-rich cells in the gills that function to increase salinity tolerance in fish (Hoar 1988; Uchida et al. 1996). In contrast with smolts, there were no significant increases in gill Na^+,K^+-ATPase activity in wild-reared parr captured between March and May, while condition factor increased in parr during spring as expected with increasing food availability.

Seasonal effects

In addition to the characteristic increase in gill Na^+, K^+-ATPase activity, a number of other enzymes changed in activity level over the course of the study. While we refer here

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Table 1. Mean values (±SE) of biochemical indices (U·g wet mass^{-1}) measured in Atlantic salmon parr and stream- and hatchery-reared smolts in March, April, and May–June of 1994.

	Parr			Stream-reared smolts			Hatchery-reared smolts		
	March	April	May–June	March	April	May–June	March	April	May–June
N	8	9	10	10	5	20	12	11	11
Heart LDH	118.5 (21.87)	100.06 (5.29)	123.72 (2.90)	127.82 (8.72)	91.64 (2.39)	113.07 (3.73)	103.98 (3.63)	124.08 (9.01)	94.19 (5.42)
Liver PFK	0.90 (0.24)	1.33 (0.18)	0.75 (0.07)	0.82 (0.17)	1.05 (0.28)	0.88 (0.07)	0.82 (0.11)	0.73 (0.12)	1.11 (0.11)
White muscle HOAD	1.27 (0.17)	1.24 (0.18)	1.25 (0.12)	1.05 (0.12)	1.00 (0.10)	1.47 (0.16)	1.02 (0.06)	1.25 (0.14)	1.18 (0.07)

Note: *N* is number of individuals.

to these as seasonally affected parameters, it should be noted that they are actually being affected by a variety of season-linked factors, likely including temperature, photoperiod, and food availability. Heart and liver CS increased in all three juvenile salmon groups throughout the spring. This suggests an overall increase in metabolic respiratory capacity in the two tissues, probably a reflection of increased mitochondrial volume (Blake et al. 1984; Moyes 1996). Liver HOAD also increased in all three groups over the course of the study; however, there were no changes in this enzyme in the other tissues examined. This suggests an increased capacity to mobilize fatty acids (elevated lipolysis) in the liver, as has been demonstrated for coho salmon smolts (Sheridan et al. 1985). Liver LDH activity decreased in all three groups, particularly smolts, over the course of the study, suggesting a decreased reliance on lactate–pyruvate conversion as spring progresses. Liver LDH has been shown to decrease during smolting and has been implicated in low concentrations of blood glucose and liver glycogen via decreased gluconeogenesis (Plisetskaya et al. 1994; Ji et al. 1996).

CSI increased in smolts over the course of the study, while parr CSI remained unchanged. This is in accord with Poupa et al. (1974) who found that heart growth is accelerated (relative to whole-body growth) during salmon smolting. During this phase, the cardiac compact shell rapidly increases in mass, while the spongy cardiac tissue growth rate remains unchanged relative to parr and ocean-stage salmon growth rates. It may be that the increased heart mass of smolts is necessary for the cardiac output demands of the constantly swimming, schooling life history that is characteristic of salmonids at sea.

Influence of hatchery rearing

In several of the parameters measured, we found significant differences between smolts reared in the hatchery and those that underwent smolting in the wild. Both liver CS and HOAD activities were higher in stream-reared smolts than in hatchery-reared smolts. However, these lower enzyme activities in hatchery-reared smolts may be offset by their larger livers (higher HSI than in stream-reared smolts). Sheridan et al. (1985) suggested that the increased lipolysis occurring in smolts is a response to the metabolic demands of smolting exceeding food input. If this is the case, then the elevated levels of lipolysis suggested by our data for stream-reared smolts may reflect the difference in food availability between stream- and hatchery-reared smolts with subsequent biochemical, and perhaps behavioral, consequences that may occur when hatchery smolts are released into the wild (as in our May samples).

Hatchery- and stream-reared smolts showed reversed patterns of heart PFK activity. In hatchery smolts, heart PFK was highest in March, while in stream-reared smolts (and parr), the enzyme activity was low early in the spring and was highest in May. The common pattern between parr and stream-reared smolts suggests that the increasing heart PFK activity may be influenced more by natural-stream rearing than by life history stage.

Heart HOAD and mass also differed between the two smolt groups. CSI in stream-reared smolts was consistently higher than in hatchery-reared smolts. Exercise has been shown to influence heart size in some species (Farrell et al.

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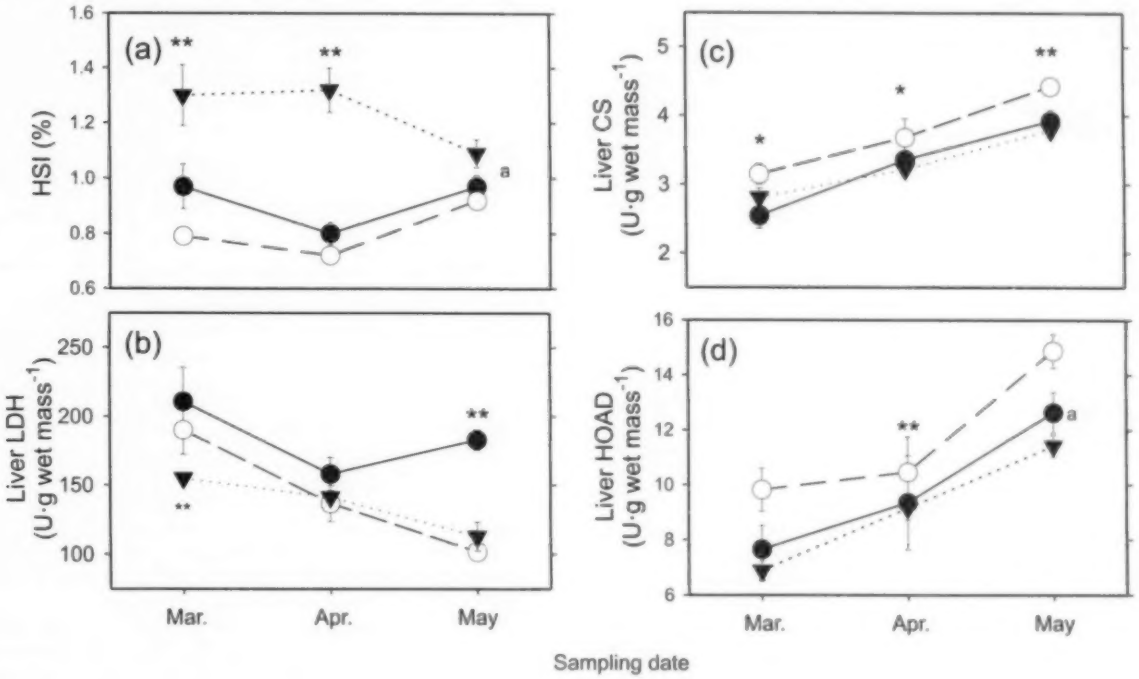
Fig. 4. (*a*) HSI, (*b*) liver LDH activity, (*c*) liver CS activity, and (*d*) liver HOAD activity of Atlantic salmon parr (●), stream-reared smolts (○), and hatchery-reared smolts (▼) sampled during March, April, and May–June 1994 in the Connecticut River watershed. Data are means ± SE. A single asterisk indicates a significant difference from parr activity at a given sampling time and a double asterisk indicates a significant difference from the other two juvenile salmon groups at a given sampling time. Statistics indicate ANOVA and post hoc testing with $\alpha = 0.05$.



1991), and it is possible that the differences that we observed were a function of the greater activity regime that is probable for stream-reared fish. However, it should be noted that increased heart weight with exercise is not a consistent phenomenon in fishes (Davison 1997), and the potential impact of exercise on heart weight in juvenile Atlantic salmon should be investigated. The difference observed in the present study may have developed soon after release into the wild as fry and been maintained thereafter. Additionally, the increasing heart size (CSI) of smolts has the effect of exaggerating the PFK elevation in wild-reared smolts, if these data are considered on a whole-organ basis, further emphasizing the differences between wild- and hatchery-reared smolts.

The patterns of PFK and LDH activities in white muscle, which differ in the two smolt groups, suggest a temporal shift in smolt enzyme regulation. In both white muscle PFK and white muscle LDH, there is a peak in hatchery smolt activity in April, followed by a decline in May. In stream-reared smolts the elevation in activity occurs in May. In the case of white muscle LDH, despite the early elevation of activity in hatchery smolts, the increase in activity may be a seasonal response common to all groups, since parr also show an elevation of activity in May. This again suggests that the wild-rearing habitat differs from that of the hatchery in its effect on metabolic parameters. In the case of white muscle PFK, however, the elevation in enzyme activity also appears to be related to life stage. Parr show an increase in white muscle PFK during May, but it is not as great as that seen in the smolt groups, and the level of activity in parr is much lower than in the smolts. It may be that the peak in white muscle PFK is related to the cortisol peak that is characteristic of the parr–smolt transformation (Hoar 1988; Shrimpton et al. 1994*b*). Cortisol is involved in stimulating or maintaining increased plasma glucose in response to stress. Atlantic salmon smolts exhibit higher plasma cortisol and glucose than parr when given an identical handling stress (Carey and McCormick 1998). PFK is a key enzyme in glycolysis and its elevation may indicate an upregulation of the glycolytic pathway in order to facilitate glucose utilization and homeostasis during smolting. Shrimpton et al. (1994*b*) found a temporal displacement between the cortisol concentration peaks in hatchery- and wild-reared Atlantic salmon smolts similar to that found in our study for white muscle PFK. McCormick and Bjornsson (1994) found higher levels of plasma cortisol in migrating stream-reared smolts than in smolts reared and kept in a hatchery. It is possible that the increased white muscle PFK of smolts is part of an adaptation for increased burst swimming ability that evolved due to increased mortality from swimming predators during downstream migration and in the ocean.

In conclusion, our data suggest that, although they undergo some of the same metabolic changes as stream-reared smolts, Atlantic salmon smolts produced in hatcheries respond to a different degree, in a temporally different manner, or show an altered pattern of metabolic change compared with fish reared in the wild. While the implications for long-

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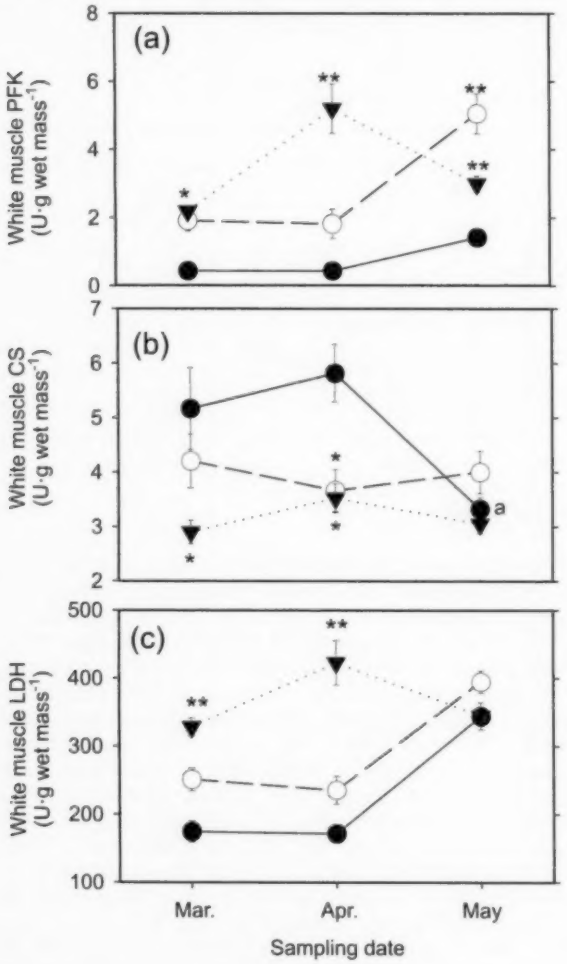
Fig. 5. White muscle (*a*) PFK activity, (*b*) CS activity, and (*c*) LDH activity of Atlantic salmon parr (●), stream-reared smolts (○), and hatchery-reared smolts (▼) sampled during March, April, and May–June 1994 in the Connecticut River watershed. Data are means ± SE. A single asterisk indicates a significant difference from parr activity at a given sampling time, a double asterisk indicates a significant difference from the other two juvenile salmon groups at a given sampling time, and "a" indicates a significant difference between smolt groups, neither of which is different from parr, at a given sampling time. Statistics indicate ANOVA and post hoc testing with $\alpha = 0.05$.



term survival and reproductive success are unclear, our findings suggest that smolts reared in hatcheries differ substantially in their physiology from smolts reared in the wild. If some or all of these metabolic changes are indeed adaptive, perhaps observable in the differing body form or swimming capacities of parr and smolts, then altered metabolic patterns occurring under hatchery conditions may be involved with reduced survival or return rates of hatchery-reared fish. More investigation of the physiological effects of hatchery rearing on fitness is warranted. White muscle PFK and CSI exhibited differences as a function of both smolting and environment and may be especially useful for further examination of the impact of rearing and release on smolt development and survival.

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Functional processes versus state variables: interstitial organic matter pathways in floodplain habitats

C. Claret, A.J. Boulton, M.-J. Dole-Olivier, and P. Marmonier

Abstract: We assessed the potential rates of two microbial processes, cellulose decomposition potential (CDP) and hydrolytic activity, to explore the relationship of these functional measurements with several state variables of organic matter. Samples were collected from two interstitial sites in the main channel of the Rhône River and 10 sites on the alluvial floodplain representing five habitat types defined by sediment size (fine versus coarse sediments) and interstitial water origin (surface water versus groundwater). Although sites with fine sediments had more interstitial total organic matter, refractory and biodegradable dissolved organic carbon concentrations did not differ among habitat types. Unlike the floodplain, the main channel had high CDP and low hydrolytic activity. In the floodplain, functional measurements varied consistently, and both CDP and hydrolytic activity were lowest at the sites with coarse sediments. Our data imply that microbially mediated processes are different in the main channel and the floodplain and that low levels of organic matter in the coarse sediments are probably due to slow rates of accrual rather than rapid rates of decomposition. Furthermore, the lack of correlation between functional variables and dissolved organic carbon concentrations illustrates the dangers of interpreting ecosystem processes or ecological integrity based solely on state variables.

Résumé : Nous nous sommes intéressés à deux processus microbiens (considérés comme des variables "fonctionnelles"), potentiel de dégradation de la cellulose (CDP) et activité hydrolytique, et à leur adéquation avec les teneurs en matière organique dans les sédiments et dans l'eau (i.e., "variables d'état"). Deux sites ont été échantillonnés dans le chenal principal du Rhône et dix sites dans la plaine alluviale, ces sites représentant cinq type d'habitats définis par la taille des sédiments (sédiments fins vs. sédiments grossiers) et l'origine de l'eau interstitielle (surface vs. souterraine). Dans les sites à sédiments fins les teneurs en matière organique totale sont plus élevées que dans les sites à sédiments grossiers, alors que les concentrations en carbone organique dissous réfractaire et biodégradable ne varient pas entre les habitats. Le chenal se distingue des autres stations de la plaine alluviale par des valeurs de CDP élevées et une faible activité hydrolytique. Dans la plaine alluviale, les deux variables "fonctionnelles" varient dans le même sens et l'activité hydrolytique comme le CDP étaient plus faibles dans les habitats à sédiments grossiers. Ils semblent donc que les processus microbiens mis en jeu ne soient pas les mêmes dans le chenal et dans la plaine alluviale et que les faibles teneurs en matière organique dans les sédiments grossiers sont dus à une faible accumulation plutôt qu'à une décomposition rapide. En outre, l'absence de corrélation entre les variables fonctionnelles et la fraction dissoute de la matière organique montre qu'il peut être périlleux d'interpréter le fonctionnement d'un écosystème en ne considérant que des variables d'état.

Introduction

Ecologists are often forced to infer ecological processes from "snapshot" measurements of state variables (see Zedler 1996), a perilous undertaking when the spatial or temporal scale of measurement does not coincide with the relevant process. This dilemma has been acknowledged in general ecology for some time (e.g., Greig-Smith 1986) and is evident in many aspects of river ecology (Minshall 1988; Palmer and Poff 1997), especially microbial studies (Boon 2000). Furthermore, the relationship between the state variables and their dynamic processes is seldom simple or direct and may include time lags in response that are difficult to detect (Dahm et al. 1998). Finally, analysis of this relationship has significant management implications because measuring processes rather than patterns probably provide better indicators of ecological integrity (sensu Karr 1996) in assessing river "health" (Bunn et al. 1999).

We define a "state variable" as a variable that is estimated from an instantaneous snapshot measurement (e.g., dissolved

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oxygen saturation, organic matter concentration) and a "functional variable" as one that estimates the *rate* or *potential* of an ecological process (e.g., respiration rate, cellulose decomposition potential (CDP)). By combining these two types of variables, our understanding of inputs, storage, transformations, and exports of material and energy in ecosystems is enhanced considerably (Bott and Kaplan 1985; Baker 1986; Dahm et al. 1998). However, technical limitations (time constraints, sample disturbance, excessive cost) and perhaps some inertia to vary traditional methods have slowed the widespread adoption of an integrated approach using both state variables and functional variables to help understand ecological processes. Thus, most broad-scale studies of lowland rivers, their floodplain wetlands, and their aquifers infer prevalent ecological processes from instantaneous collections of physical, chemical, and biological data (e.g., Dole-Olivier et al. 1994; Tockner and Bretschko 1996).

The few efforts made to assess potential rates of microbial processes are generally based on time-consuming and (or) expensive methods that give limited information for a global quantitative estimation of functional processes and are difficult to use routinely and extensively in large-scale studies. Recently, studies on carbon dynamics in freshwater systems have benefited from the application of functional process methods originally developed for terrestrial biomes. For example, the use of hydrolytic activity (e.g., fluorescein diacetate (FDA) analysis, Marmonier et al. 1995; Claret and Fontvieille 1997) or CDP (e.g., cotton-strip assays, Hildrew et al. 1984; Boulton and Quinn 2000) now enables the integration of state and functional variables in aquatic systems.

At the scale of a single geomorphological unit (1–100 m), such as a riffle or gravel bar, substrate particle size and directions of hydrologic exchanges influence organic matter content, oxygen availability, and thus the composition of subsurface assemblages (Marmonier and Dole 1986; Dole-Olivier 1998). At the floodplain scale (1 to >5 km), trends in water chemistry, sediment characteristics, and interstitial fauna occur with increasing lateral distance from the main river out on the floodplain as well as the degree of connectedness to the groundwater (e.g., Marmonier et al. 1992; Dole-Olivier et al. 1994). For instance, the Rhône River floodplain is characterized by a series of wetland habitats formed by cutoff channels of increasing age and distance from the main channel. Floodplain habitats in these channels possess different-sized sediment particles, different concentrations of organic matter, and varying connectedness to the groundwater as a complex result of natural fluvial processes and human activities (embankment and regulation, Amoros and Roux 1988). Given these marked differences in hydrology and geomorphology of the Rhône floodplain habitats, concurrent differences in the rates of microbially mediated processes might be expected, as reported at finer scales (e.g., Pusch and Schwoerbel 1994; Findlay and Sobczack 1996; Dahm et al. 1998).

In this study, we address two major questions: (*i*) the influence of spatial heterogeneity of physical parameters (sediment size, water origin) on functional processes and (*ii*) the relationship between state variables and functional variables in ecological studies at a large scale (the floodplain). We addressed the first aim using technically simple methods to assess the potential rates of two microbial processes, organic matter decomposition (estimated by CDP) and hydrolytic activity (estimated by FDA hydrolysis), in the sediments of wetlands varying in particle size and water inputs. As there is a large surface area for microbial biofilms on fine particles, we hypothesized that both processes should be fastest in fine-sediment habitats. Furthermore, we expected that active circulation of surface or groundwater would accelerate these processes relative to stagnant conditions because of higher inputs of dissolved oxygen and nutrients (Dahm et al. 1998).

The second question was addressed by comparing how successfully the state variables of organic matter (total organic matter (TOM), dissolved organic carbon (DOC)) matched estimates of the functional variables for organic matter dynamics (CDP, FDA) in interstitial habitats. DOC was further subdivided into refractory and biodegradable fractions because we hypothesized that patterns in these should more closely match functional measurements of decomposition. This has been observed at a finer scale within the main channel of the Rhône River (Marmonier et al. 1995; Claret et al. 1997) but not explored at the floodplain scale.

Materials and methods

Study area

The alluvial floodplain of the upper Rhône River is formed of fluvioglacial sediments and Würmian morainic complex (Creuzé des Châtelliers 1991). A mosaic of surface wetlands exists, deriving water from the main channel, alluvial aquifers, or a combination of the two. "Primary" anabranches, most closely linked to the river, tend to have coarser sediments than more distant "secondary" anabranches that are seldom flushed when the Rhône floods. At low or base flow in the main channel, groundwater upwells into sections of the anabranches, depending on subsurface flow paths. Amounts of interstitial organic matter are usually greatest in the secondary anabranches and in wetlands more distant from the main channel (Amoros et al. 1987; Rostan et al. 1987).

Two sites were sampled in the main channel of the Miribel channel (Fig. 1), a bypassed section of the Rhône River (described in Dole-Olivier and Marmonier 1992). Site 1 was located in the middle of a gravel bar situated on the right bank of the main channel and fed by groundwater. Site 2 was located upstream of this gravel bar with infiltration of surface water.

Ten sites were chosen in three anabranches of the alluvial floodplain to represent all four combinations of water origin (surface water versus groundwater) and sediment features (fine sediments versus coarse sediments) with a further pair of sites in fine sediments that lacked any form of hydrological exchange (Fig. 1; Table 1). La Chaume backwater (Sites 3 and 4) is a secondary anabranch with fine sediments and negligible hydrological exchange that was isolated from the main channel during the seventeenth and eighteenth centuries. In contrast, the Îles Nouvelles and the Méant backwaters are primary anabranches, comprising braided side-arms close to the main channel. The Iles Nouvelles anabranch (Sites 5 and 7) has been isolated from the main channel by embankments built during the nineteenth century. This backwater is fed by deep groundwater from an aquifer located on the northern side of the valley (Plénet et al. 1992). Site 5 has fine sediment and is fed by groundwater via a cluster of large interstitial springs that wells up through the bed sediments whereas Site 7 has fine sediment and receives surface water inputs.

The Méant anabranch (Fig. 1) has been isolated from the active channel at its upstream end since 1940 by deposition of an alluvial plug (Dole-Olivier 1998) but remains permanently connected to the

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Fig. 1. Location of sampling sites. Sites 1 and 2 are in the main channel, Sites 3 and 4 have fine sediments and no exchange, Sites 5 and 6 have fine sediments with groundwater inputs, Sites 7 and 8 have fine sediments with surface inputs, Sites 9 and 10 have coarse sediments with groundwater inputs, and Sites 11 and 12 have coarse sediments with surface water inputs.

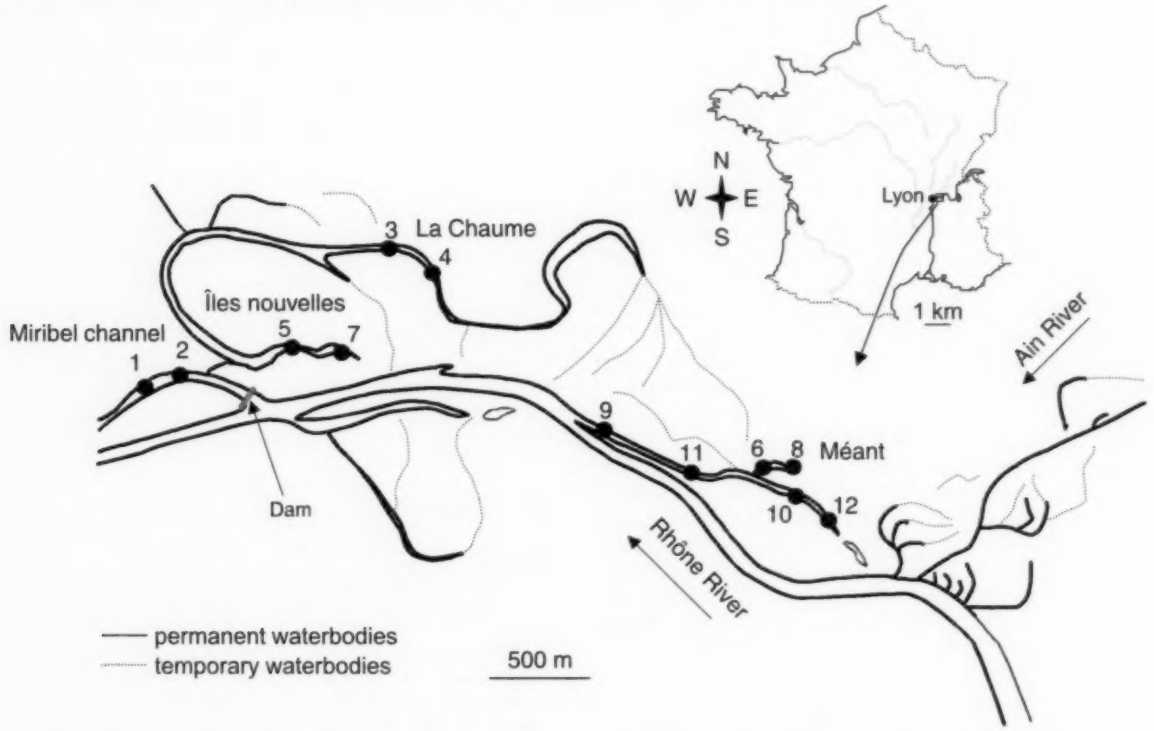

Table 1. Site codes used to identify sediment size and water origin at 12 sites on the Rhône River floodplain and main channel.

Sites	Code	Sediment size	Water origin
1 and 2	MC	Coarse	
3 and 4	F0	Fine	No hydrological exchange
5 and 6	FG	Fine	Groundwater
7 and 8	FS	Fine	Surface
9 and 10	CG	Coarse	Groundwater
11 and 12	CS	Coarse	Surface

Rhône River at its downstream end. This anabranch is supplied by seepage water from the Rhône River and the Ain River that mixes with deep groundwater. Two of the sites have fine sediments and receive either groundwater (Site 6) or surface water (Site 8). The other sites are characterized by coarse sediments fed by groundwater (Sites 9 and 10) or by surface water (Sites 11 and 12).

Field sampling, water chemistry, and sediment size analyses

Interstitial water and sediments were collected in October 1998 using a peristaltic handpump from temporary wells inserted to 20 cm. Temperature and specific conductance (thermoconductimeter WTW LF 92) and dissolved oxygen concentrations (oxymeter WTW OXI 91) were measured directly in the field. Triplicate water samples were collected in 1-mL Eppendorf tubes for water chemistry analyses and in 200-mL acid-washed plastic bottles for DOC analyses. Triplicates samples of interstitial sediments were stored in 50-mL acid-washed plastic vials for TOM and hydrolytic activitiy analyses.

Water samples were refrigerated during the return to the laboratory where nitrate, sulfate, phosphate, and chloride concentrations were determined with a capillary ion analyser (Waters Co.). For sediment particle size analyses, single grab samples of at least 500 g were collected near the temporary wells. Surface sediments (top layer of 5 cm) were sieved into eight size-classes: silt and clay (<50 µm), very fine sand (50–125 µm), fine sand (125–250 µm), medium sand (250–500 µm), coarse sand (500 µm – 1 mm), very coarse sand (1–2 mm), gravel (2–16 mm), and pebble (>16 mm). For each sediment sample, the median grain diameter ($D50\%$) was determined from the 50th percentile on a graph of cumulative percentages of each size fraction by weight.

State variables of organic matter

In the laboratory, a 120-mL aliquot of each water sample was filtered on a 0.2-µm-mesh acetate filter (Millipore GSWP type) that had been previously rinsed thrice with 10 mL of distilled water and once with 10 mL of the sample. To determine initial DOC concentrations (t_0), 10 mL was stored in a preashed (2 h at 550°C) glass bottle, capped with an aluminum stopper, and immediately frozen. The remaining filtered water was used to determine refractory dissolved organic carbon (RDOC) concentrations. After injection of an inoculum (1% final concentration) prepared from autochthonous bacteria (Servais et al. 1987, 1989), water samples were incubated at 15°C for 30 days (t_{30}) and 35 days (t_{35}). After each incubation, 10 mL was filtered on a 0.2-µm-mesh acetate filter (Millipore GSWP type) and the filtrate was analysed with a Dorhmann-DC 80 carbon analyser to determine DOC and RDOC concentrations. Biodegradable dissolved organic carbon (BDOC) was determined as the difference between DOC and RDOC concentrations for each sample. TOM content of sediments (10-g subsample) was deter-

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mined as loss on ignition during 4 h at 550°C (Bretschko and Leichtfried 1987) and expressed as ash-free dry mass.

Functional variables

Cellulolytic activity

To estimate CDP, we used a modified version of the cotton-strip assay (Boulton and Quinn 2000). Standard Shirley soil burial test fabric was prepared by autoclaving the material at 120°C for 15 min before cutting it into strips measuring 55 mm (warp) × 32 mm (weft), leaving several threads either side of the marker threads that are exactly 30 mm (100 threads) apart. At one corner, a small hole was made with a needle for the attachment of a fishing line leader so that the strips could be detected for recovery.

At each site, six strips were buried to a depth of 20 cm, parallel to the anticipated groundwater flow path. Strips were inserted using a thin spatula to minimize sediment disturbance. The fishing line leader extended to the surface to mark the exact location of the strip. Strips were retrieved 21 days later, taking care to remove the sediments from around the strip without tugging on the fishing line leader. They were folded in aluminum foil for return to the laboratory where they were gently washed to remove any adhering sediment and air-dried before reweighing. After removal of the lateral threads either side of the markers and a single marker thread (ensuring a weft of 100 threads), tensile strength loss was determined using a tensometer. The cotton-rotting rate (CRR, per year), determined according to the function derived by Hill et al. (1985), was used as an estimation of the CDP.

Hydrolytic activity

Microbial activity was determined by the degradation of the FDA (Sigma Chemicals, St. Louis, Mo.) (Fontvieille et al. 1992). Three millilitres of phosphate buffer (pH 7.6) and 0.1 mL of FDA were added to 1 g of wet sediments in an acid-washed glass vial. The samples were gently shaken and incubated until a faint green coloration appeared (about 30–60 min) when the reaction was stopped with 3 mL of $HgCl_2$ (400 mg·L^{-1}) and the samples were stored in a freezer. Absorbance was measured with a spectrophotometer at 490 nm. Microbial activity is expressed as micromoles of FDA hydrolysed per hour per gram of sediment dry mass. Samples for sediment FDA activity determinations were collected from each site next to the cotton strips.

Data analyses

Data were tested for normality using the Wilk–Shapiro test (Analytical Software 1996) and log transformed before further statistical analyses. Means of log-transformed data were compared among sites and habitat types using one-way analyses of variance followed by Tukey's tests if significant differences ($P < 0.05$) occurred. Univariate statistical analyses were performed using Statistix (Analytical Software 1996).

Principal components analysis (PCA) was conducted using ADE-4 software to explore the relationship among the sites in terms of their physicochemical features and the state and functional variables of organic matter. Data were log transformed before analysis. As the majority of total variance was explained by the first two axes (45%), vectors of the environmental variables in this ordination space are compared with the site replicates ($n = 3$) for each location. We plotted all of the replicates to illustrate the within-site variance in ordination space for comparison with among-site variation.

Results

Sediment size

Median grain size ($D50\%$) ranged from 0.05 mm at Site 7 to more than 7 mm in the main channel and at Sites 11 and 12 (Table 2). The distinction between the fine ($D50\% <$ 1 mm) and coarse ($D50\% > 4$ mm) sediment categories is clearly evident.

Patterns of physicochemical, states, and functional variables

Differences among the stations are evident on the PCA ordination plot where the first two axes account for 45.1% of the total variance (Fig. 2). The first axis (C1, 30.3%) is strongly weighted by chloride, TOM, sulfate, and the two functional variables hydrolytic activity (FDA) and CRR. This axis separates the floodplain habitats with coarse sediments (low scores on C1) from sites with fine sediment and from the main channel sites (MC, with coarse sediments) where most of the above-mentioned variables attained high values. This is especially true for TOM and the two measures of microbial processes that reached their highest values at Sites 3 and 4 located at the extreme of the positive side of the C1 axis (Fig. 2). Temperatures were generally close to 12.5°C, but the groundwater-fed Site 10 was slightly cooler (Table 2). Sulfate concentrations were generally high (up to 13 mg·L^{-1}) (Table 2) and varied little among the sites because of the geological characteristics (gypsum substratum) of much of the central Alps.

The second axis (C2, 14.9%) mainly accounts for dissolved oxygen and RDOC concentrations on the positive side and specific conductance on the negative side. This axis distinguishes Site 2, a downwelling zone in the main channel characterized by higher oxygen concentrations (10.5 mg·L^{-1}) and lower specific conductance values (382 µS·cm^{-1}), from the other sites with less oxygen (1.2–7.9 mg·L^{-1}) and higher conductivities (>400 µS·cm^{-1}) (Table 2).

State variables

BDOC did not vary significantly among the sites ($F_{11,19} = 0.97$, $P = 0.50$) or habitat types ($F_{5,25} = 1.33$, $P = 0.28$) (Fig. 3*a*). Variances were especially high in the heterogeneous sediments of the main channel (Sites 1 and 2), in the organically enriched sediments at Site 3, and at the two sites with groundwater input and coarse sediments (Sites 9 and 10). Conversely, RDOC was significantly higher ($F_{11,21} = 3.54$, $P = 0.0062$) at Site 2 (main channel with coarse sediments) than at Site 5 and, to a lesser extent, at Site 11 (Fig. 3*b*). These differences reflect differences in local conditions rather than trends linked to sediment particle size or water origin. TOM content differed significantly among sites ($F_{11,24} = 8.10$, $P < 0.0001$). There was less interstitial TOM in the floodplain sites with coarse sediments (Sites 9, 10, and 12) than at sites with fine sediments (Fig. 3*c*). There is no discernible trend in TOM linked to water origin (Fig. 3*c*).

Functional variables

The highest CRRs were measured in the main channel sites (Sites 1 and 2) (Fig. 4*a*). In the floodplain, CRR values were similar in sites that shared similar characteristics (e.g., Sites 3 and 4, Sites 5 and 6) but differed significantly ($F_{11,24} = 13.22$, $P < 0.0001$) among habitat types according to grain size (fine sediment versus coarse sediment). Variances within habitat type were generally low except at Site 4 where hydrological exchange was limited.

Hydrolytic activity also varied significantly among sites ($F_{11,24} = 21.58$, $P < 0.0001$). Microbial activity was low in

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Table 2. Environmental features of the 12 sites investigated on the Rhône River and its floodplain in 1998 (mean ± SD, $n = 3$).

Site	Habitat type	Code	*D*50% (mm)	Temperature (°C)	Specific conductance ($\mu S \cdot cm^{-1}$)	O_2 ($mg \cdot L^{-1}$)	Cl^- ($mg \cdot L^{-1}$)	SO_4^{2-} ($mg \cdot L^{-1}$)	NO_3^- ($mg \cdot L^{-1}$)	PO_4^{2-} ($mg \cdot L^{-1}$)
	Rhône River	Surface		13.1	380	11.1	4.4	12.3	2.4	0.06
1	Main channel	MC	7.3	12.5±0.2	591±5	2.5±0.7	7.93±0.06	13.07±0.38	5.50±0.72	0.08±0.03
2	Main channel	MC	7.2	13.2±0.1	382±4	10.2±0.4	4.63±0.67	12.00±0.70	2.63±0.25	0.06±0.01
3	Floodplain	F0	0.47	12.5±0.3	568±13	1.2±0.7	8.33±0.80	6.27±1.55	6.20±4.75	0.07±0.04
4	Floodplain	F0	0.32	12.5±0.3	626±39	1.9±0.8	9.03±0.38	9.90±3.48	8.77±5.41	0.07±0.55
5	Floodplain	FG	0.08	12.9±0.2	524±1	7.9±0.3	7.00±0.10	5.40±0.10	11.50±0.35	0.06±0.01
6	Floodplain	FG	0.18	12.6±0.1	443±10	4.1±0.3	3.40±0.17	2.87±0.31	4.83±0.76	0.07±0.04
7	Floodplain	FS	0.05	12.4±0.2	614±50	1.3±0.9	6.67±0.45	3.47±0.84	4.50±1.83	0.11±0.03
8	Floodplain	FS	0.28	12.5±0.1	521±78	3.1±2.3	3.83±0.38	2.02±1.67	2.60±2.19	0.13±0.05
9	Floodplain	CG	6.2	12.3±0.5	473±3	6.9±0.3	3.93±0.23	3.03±0.23	6.07±0.72	0.07±0.01
10	Floodplain	CG	4.6	10.5±0.3	414±0	1.9±0.4	3.20±0.10	2.33±0.10	1.60±0.10	0.08±0.05
11	Floodplain	CS	7	12.6±0.3	545±31	3.9±2.0	4.60±1.40	6.33±2.84	7.50±2.48	0.08±0.03
12	Floodplain	CS	7.1	11.3±0.2	424±1	3.3±0.2	2.93±0.59	2.00±0.10	2.17±0.35	0.09±0.04

Note: *D*50% is the median size diameter. See Table 1 for site code abbreviation.

Fig. 2. PCA ordination plot of the environmental parameters. (*a*) Ordination of the physicochemical, state, and functional variables. Values in parentheses along the axes are the percentage of total variance explained by each principal component. Cond, specific conductance; T°C, temperature; O_2, dissolved oxygen concentrations; BDOC, biodegradable dissolved organic carbon; RDOC, refractory dissolved organic carbon; TOM, total organic matter content; CRR, cotton-rotting rate; FDA, hydrolytic activity. (*b*) Ordination plot of the site and replicates on the first two axes of a PCA. Open circles, fine sediments; solid circles, coarse sediments; hatched circles, main channel sites. Numbers refer to sites as in Fig. 1. See Table 1 for definitions of the abbreviations.

the main channel, while rates of FDA hydrolysis followed broadly similar patterns to those of the rates of cotton decay in the alluvial floodplain (Fig. 4*b*). In the sites with coarse sediments (Sites 9–12), both hydrolytic activity and CRR were consistently low, with low variability among sites (Fig. 4*b*). In contrast, FDA was rapidly hydrolysed in the sites with fine sediments (especially at Sites 3, 4, and 6) but did not reflect differences in water origin (groundwater versus surface water). Generally, variances in hydrolytic activity within each habitat type were greater than those observed for CRR.

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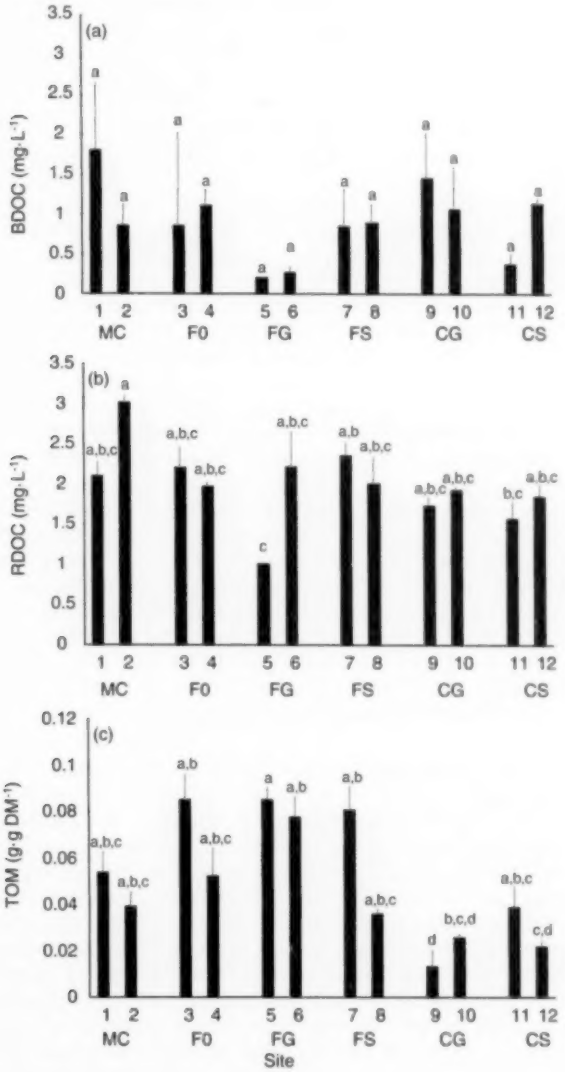
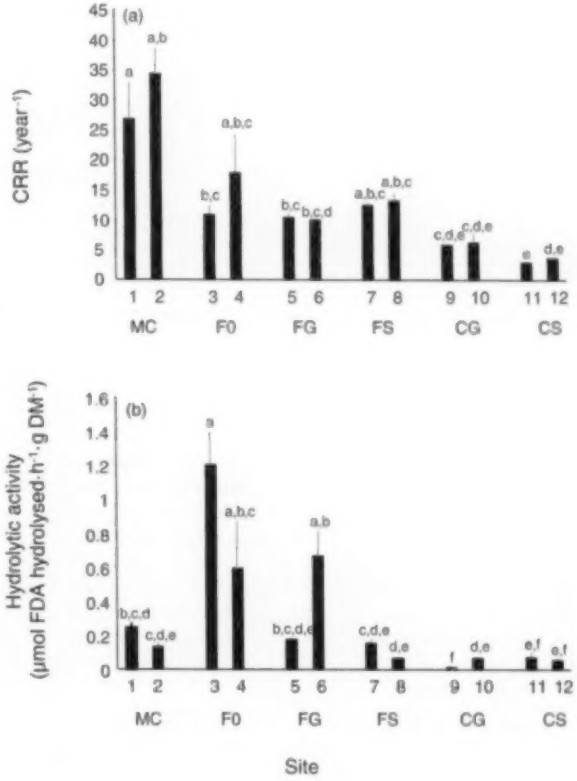
Fig. 3. Concentrations of (*a*) BDOC ($P = 0.5016$) and (*b*) RDOC ($P = 0.0062$) of interstitial water and (*c*) content of TOM ($P < 0.0001$) of sediments at each site. DM, dry mass. All data are means + 1 SE ($n = 3$). Values with the same letter are not significantly different ($P > 0.05$). See Table 1 for definitions of the abbreviations.



Interstitial hydrolytic activity and CRR across the floodplain habitats were correlated ($r = 0.45$, $P = 0.006$). The influence of sediment particle size is also evident, with low CRR and low FDA activity occurring in coarse sediments. However, the sites in the main channel with coarse sediments grouped with samples from the floodplain sites with fine sediments (Fig. 5). When these main channel stations (Sites 1 and 2) are excluded, the correlation is stronger ($r = 0.48$, $P = 0.001$), illustrating the potential influence of floodplain-scale issues on the relationship between these functional variables.

Fig. 4. (*a*) CRR ($P < 0.0001$) and (*b*) hydrolytic activity ($P < 0.0001$) at each site. DM, dry mass. All data are means + 1 SE ($n = 3$). Values with the same letter are not significantly different ($P > 0.05$). See Table 1 for definitions of the abbreviations.



Correlations between state and functional variables

When all sites are considered together, CRR correlated significantly with the state variables of RDOC ($r = 0.48$, $P = 0.004$) and TOM ($r = 0.41$, $P = 0.012$). However, hydrolytic activity was uncorrelated with either BDOC or RDOC but did correlate strongly with TOM ($r = 0.75$, $P < 0.0001$).

Discussion

Influence of water origin and sediment particle size

The source of the water and the sediment particle size had minimal influence on the state variables measured in this study. In particular, minimal differences were observed for both fractions of DOC according to physical characteristics of the sites despite their variable nature and geomorphic origins. In the alluvial floodplain of the Rhône River, the biodegradable fraction was highly variable, ranging from 13 to 58% of total DOC concentrations. These values are close to those observed in a riverine wetland (Mann and Wetzel 1995) and indicate that microbial activity is not restricted by a lack of appropriate substrate. At a fine scale, BDOC concentrations result from the net balance between local consumption and

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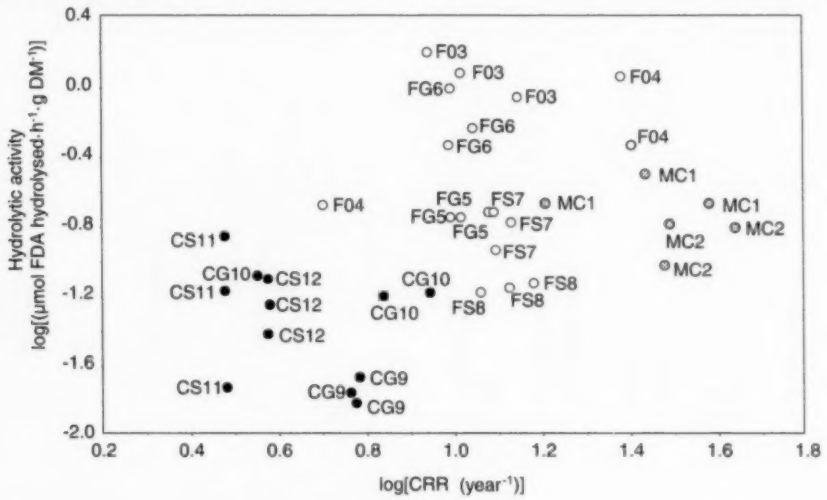
Fig. 5. Pearson's correlations between CCR and hydrolytic activity for all sampling sites (n = 36, P = 0.006). DM, dry mass. See Table 1 for definitions of the abbreviations.



local production, two dynamic processes constantly oscillating in response to a variety of environmental constraints. Where activity is very high (as in the fine sediments), decreases in dissolved oxygen content induce BDOC production whereas BDOC is not assimilated in regions of low activity in coarse sediments. Thus, as a result of two very different processes (i.e., production, reduced assimilation), the total concentrations of BDOC remain similar and the prevailing ecological process is undetectable from a snapshot measure of this state variable.

In contrast with the dissolved fractions, TOM content of the interstitial sediments correlated with physical heterogeneity in sediment size across the alluvial floodplain habitats. The relationship between organic matter content and sediment size is well documented (e.g., Kondratieff and Simmons 1984). Our findings are consistent with the study by Rostan et al. (1987) who observed a reduction in organic carbon content with increasing proportions of coarse sediments across the floodplain of the Rhône River.

In our study, hydrolytic activity and CRR displayed convergent trends, although these functional variables probably differ in their enzymic and metabolic pathways. At the floodplain sites, differences in the rates and potentials of these functional variables were more strongly correlated with sediment particle size than with the origin of interstitial water (surface versus groundwater). As hypothesized, coarse sediments supported lower rates of hydrolytic activity and CDP than fine sediments. Fine particles offer a greater surface area for biofilm development than coarse particles (Hargrave 1972; Bärlocher and Murdoch 1989), although there is also a greater potential for microscale variations in degradative pathways (Dahm et al. 1998). The habitats varied in dissolved oxygen content, but this was probably not a critical controlling factor, as cellulose decomposition and hydrolytic activity can occur under aerobic and anaerobic conditions (Schnürer and Rosswall 1982; Maltby 1988). Organic matter quality is probably the main governing factor. In this way, bacterial activity (measured as lipid synthesis) in stream sediments has been shown to be more influenced by organic matter quality than by sediment characteristics (Bott and Kaplan 1985).

In the main channel, CDP was high even though the sediments are coarse. This implies that microbially mediated processes may differ between main channel and floodplain habitats. Marked differences in microbial assemblage composition, especially the relative importance of fungi and bacteria, have been described in this sector of the Rhône River (Chergui and Pattée 1988, 1993), but the functional significance of these differences is poorly understood and is a focus for future studies.

Are state variables valid surrogates for functional processes?

When links between state and functional variables are considered in the spatial context of the entire river floodplain, both hydrolytic activity and CRR were correlated with interstitial TOM content. This relationship is probably a direct one because microbial assemblages use hydrolases to break down long-chain organic molecules present in TOM. This process implies that in habitats of the alluvial floodplain of the Rhône, low levels of organic matter in the coarse sediments are probably due more to slow rates of accrual rather than to rapid decomposition. Supplementary data on functional variables of organic matter deposition and removal are needed to confirm this hypothesis.

In most cases, we found no significant correlations between functional variables and state variables associated with dissolved fractions of organic matter. The lack of correlations indicate that at least some broad-scale processes such as CDP and hydrolytic activity cannot be predicted from snapshot measurements of BDOC or RDOC. This finding raises the more significant issue of the reliability of interpreting ecosystem processes or ecological integrity (sensu Karr 1996) based solely on measurements of state variables, even if these appear to be attractive because they can be rapidly assessed. At worst, complete reliance on such state variables

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may be misleading while at best, they seem to be a waste of resources if used alone. To our knowledge, there are not yet routine measurements of CDP or FDA hydrolysis to supplement state variables of TOM or DOC concentration and quality in monitoring programs of river health.

Interest in the use of direct measurements of ecological processes (e.g., respiration, nutrient spiraling lengths) in river health assessment is burgeoning (e.g., Bunn et al. 1999), but many of these need further technical refinement and adequate testing before they can be routinely used (Boulton 1999). Our results from the Rhône River floodplain indicate that a dual approach is needed, combining functional and state variables to obtain a more complete perception of the ecological functioning and integrity of ecosystem. At this stage, simple techniques such as the cotton-strip assay and FDA hydrolysis offer potentially useful functional variables that can be easily and quickly assessed.

It is likely that application of multiple regression and nonlinear models may reveal complex combinations of state variables that, in this case, explain significant amounts of variance in the functional variables. For example, CRR may be predicted from a linear combination of sulfate and RDOC, although the biological mechanism underlying this correlation is unclear. In this paper, we have sought to determine correlative patterns that are not only relatively simple but that are also likely to have some ecological or stoichiometric basis. Nonetheless, a water manager may be uninterested in the causal mechanisms but simply seek cheap or readily measured surrogates that may swiftly indicate significant changes in ecological functioning of a wetland or river in response to some impact. Although this may be a fruitful avenue for further study in the development of resource management techniques, we caution that heavy reliance on correlative patterns between state and functional variables without any understanding of variables that are likely to change the relationship is risky.

In conclusion, as microbially mediated processes are governed by complex environmental controls at the scale of the whole floodplain as well as the finer scales of particle and habitat heterogeneity, it is difficult to infer organic matter breakdown processes from state variables alone, even when these are chosen carefully and categorized by quality (i.e., RDOC versus BDOC). The two functional variables used in this study revealed likely "hotspots" of microbiological activity in the floodplain habitats of the Rhône River, but even these provided only limited insights. Results from the integration of both the functional and state variables preface the generation of hypotheses about rates of organic matter accrual and decomposition and reveal the spatial and temporal scales of organic matter dynamics. The ease and low cost of the two functional variables used in this study indicate their potential value in supplementing the present methods used to routinely assess the ecological integrity and health of floodplain ecosystems and, perhaps, other wetlands.

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Primary determinants of macrophyte community structure in 62 marshes across the Great Lakes basin: latitude, land use, and water quality effects

Vanessa L. Lougheed, Barb Crosbie and Patricia Chow-Fraser

Abstract: We collected water quality, land use, and aquatic macrophyte information from 62 coastal and inland wetlands in the Great Lakes basin and found that species richness and community structure of macrophytes were a function of geographic location and water quality. For inland wetlands, the primary source of water quality degradation was inputs of nutrients and sediment associated with altered land use, whereas for coastal wetlands, water quality was also influenced by exposure and mixing with the respective Great Lakes. Wetlands within the subbasins of the less developed, more exposed upper Great Lakes had unique physical and ecological characteristics compared with the more developed, less sheltered wetlands of the lower Great Lakes and those located inland. Turbid, nutrient-rich wetlands were characterized by a fringe of emergent vegetation, with a few sparsely distributed submergent plant species. High-quality wetlands had clearer water and lower nutrient levels and contained a mix of emergent and floating-leaf taxa with a diverse and dense submergent plant community. Certain macrophyte taxa were identified as intolerant of turbid, nutrient-rich conditions (e.g., *Pontederia cordata*, *Najas flaxilis*), while others were tolerant of a wide range of conditions (e.g., *Typha* spp., *Potamogeton pectinatus*) occurring in both degraded and pristine wetlands.

Résumé : Des données recueillies sur la qualité de l'eau, l'utilisation des terres et les macrophytes aquatiques dans 62 terres humides des régions côtières et intérieures du bassin des Grands Lacs indiquent que la richesse spécifique et la structure des communautés de macrophytes dépendent de la situation géographique et de la qualité de l'eau. Dans les terres humides intérieures, la source principale de dégradation de la qualité de l'eau est l'apport de nutriments et de sédiments causé par les changements dans l'utilisation des terres, alors que, dans les terres humides côtières, la qualité de l'eau est aussi influencée par le contact avec le Grand Lac adjacent et les mélanges d'eau qui s'y produisent. Les terres humides des sous-bassins des Grands Lacs d'amont, qui ont subi moins de développement et qui sont plus exposés, possèdent des caractéristiques physiques et écologiques tout à fait particulières, par comparaison avec les terres humides des Grands Lacs d'aval qui sont plus développés et moins protégés, et les terres humides intérieures. Les terres humides turbides et riches en nutriments sont caractérisées par le développement d'une ceinture de végétation émergente et la présence sporadique de quelques plantes submergées. Les terres humides de grande qualité possèdent une eau plus claire, des concentrations plus faibles de nutriments et une combinaison de taxons de plantes émergentes et de plantes à feuilles flottantes, d'une part, et d'une communauté diversifiée et dense de plantes submergées, d'autre part. Certains taxons de macrophytes se sont révélés intolérants aux conditions de turbidité et de richesse en éléments nutritifs élevées (e.g., *Pontederia cordata*, *Najas flexilis*), alors que d'autres tolèrent une gamme étendue de conditions (e.g., *Typha* spp., *Potamogeton pectinatus*) et se retrouvent dans les terres humides tant dégradées qu'intactes.

[Traduit par la Rédaction]

Introduction

Long-term changes in the macrophyte communities of individual Great Lakes coastal marshes, especially those located in settled areas of Lakes Erie and Ontario, have been well documented over the past two decades (e.g., Crowder and Bristow 1986; Klarer and Millie 1992; Chow-Fraser et al. 1998); however, the underlying factors causing these changes have rarely been investigated. These preliminary studies have indicated that year-to-year changes in areal cover of emergent vegetation are probably controlled by fluctuating water levels (Keddy and Reznicek 1986; Chow-Fraser et al. 1998), whereas growth and diversity of submergent vegetation are more likely controlled by water clarity (Lougheed et al. 1998).

The combined effects of hydrology, local bedrock geology, and wetland morphology, referred to jointly as hydrogeomorphic factors, tend to be the primary regional determinants of plant community structure in wetlands and littoral systems (e.g., Minc 1997; Thiébaut and Muller 1998; Keough et al. 1999). Where the Great Lakes basin is concerned, hydrogeomorphic variation and climatic differences associated with a total shoreline length of 12 017 km contribute to a great diversity of physical environments (Smith et al. 1991; Keough et al. 1999). These regional differences have impor-

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tant consequences for human settlement and land use patterns, with the most productive agricultural land and largest urban centers occurring south of the 46th parallel (Environment Canada and U.S. Environmental Protection Agency 1995). Consequently, although wetlands throughout the entire Great Lakes basin are at risk from non-point-source pollution (Crosbie and Chow-Fraser 1999), water level regulation (Keddy and Reznicek 1986), disturbance by nuisance exotic species such as common carp (*Cyprinus carpio*) (Lougheed et al. 1998), and internal loading of phosphorus (Chow-Fraser 1998; Mayer et al. 1999), these disturbance factors tend to predominate in the lower lakes. In particular, agricultural and urban land use in wetland catchments of the lower lakes has been shown to affect nutrient enrichment, water clarity and sediment quality (Crosbie and Chow-Fraser 1999) and will therefore likely have profound effects on submersed macrophyte growth (e.g., Phillips et al. 1978; Barko and Smart 1983; Magee et al. 1999) and distribution (Lougheed et al. 1998; Crosbie and Chow-Fraser 1999).

Macrophyte growth is limited by both water quality and sediment quality (Day et al. 1988; Barko et al. 1991). Light availability is a primary factor determining photosynthetic potential and can be reduced by nonalgal and algal turbidity, including periphytic growth (Phillips et al. 1978). As such, details on the nutrient status, sediment quality, and particulate content of the water are required to make conclusions regarding the causative effects of macrophyte community changes. Although taxonomic surveys of macrophyte communities in individual Great Lakes coastal wetlands exist (e.g., Crowder and Bristow 1986; Klarer and Millie 1992; Chow-Fraser et al. 1998), there have been no published studies that account for all of these variables and their roles in causing species replacement in the macrophyte community on a basin-wide scale. The most comprehensive study that we have found was a report by Minc (1997), who analyzed macrophyte data from 110 coastal wetlands in the U.S. waters of the Great Lakes and listed the primary determinants of macrophyte distribution as latitude, soil pH, water temperature, and turbidity; however, several important factors were excluded from this study, including trophic state and sediment fertility. In Canadian waters, Smith et al. (1991) published a study that described the differences in the physical attributes of 160 coastal wetlands in the three southernmost Canadian Great Lakes. Their study provided evidence that geology, exposure, and disturbance vary statistically among the three lakes but provided no information on water quality and taxonomic composition of submerged macrophytes that could be affected by changes in sediment and nutrient load.

The challenge facing managers is to determine the degree to which each of these hydrogeomorphic, climatic, and disturbance factors individually or in combination alters wetland plant communities. In this paper, we compare the macrophyte community composition of 62 wetlands in the Canadian part of the Great Lakes basin to examine how water quality and sediment quality affect the taxonomic composition and community structure of the macrophyte community and relate these to land use in their watershed. In addition to the 22 marshes sampled by Crosbie and Chow-Fraser (1999), located primarily along the shoreline of the lower lakes, our data set includes 40 additional coastal and inland wetlands covering all four Canadian Great Lakes. This study will contribute much needed information to help wetland managers determine the relative importance of these various factors in structuring the aquatic macrophyte community on a basin-wide scale.

Methods

Sixty-two marshes in the Great Lakes basin were visited between 1995 and 1999 and sampled for water quality and macrophyte community information. These wetlands were selected based on the amount of agricultural, urban, and forested land in their watersheds to ensure a sufficient gradient of disturbance (Crosbie and Chow-Fraser 1999). In addition, wetlands were chosen from a broad geographic range: from the St. Lawrence River just east of Cornwall, down to the Windsor–Detroit area and Lake St. Clair, and up to Lake Superior and the Ontario–Minnesota border (Fig. 1). Forty-six of these were coastal marshes (within 2 km of the Great Lakes shoreline but not separated hydrologically from the lake due to dams or waterfalls) of the upper (Huron, Superior) and lower (Ontario, Erie) lakes, while the remaining 16 wetlands were located inland within the Great Lakes – St. Lawrence River basin. All wetlands were visited once in midsummer (June 18 to July 30).

To choose the sampling location, the general character of each marsh was first assessed with a brief inspection of accessible nearshore areas. Subsequently, we selected a sheltered location (if available) containing relatively dense submergent plants (if present). All water and sediment samples were collected during daylight hours from the middle of the water column at an open-water site 3 m from the edge of macrophyte beds. Because of the large site-to-site, year-to-year, and seasonal variation in water levels, which are characteristic of Great Lakes coastal marshes (Chow-Fraser 1999), water depths in this study ranged from 5 to 260 cm, depending on wetland, time of year, and the sampling year in question; however, there were no observed effects of depth on any other parameter measured in this study.

The protocol for sampling and analysis of water samples has been documented elsewhere (V.L. Lougheed and P. Chow-Fraser, unpublished data). For each wetland, we analyzed samples for total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN) (sum of total Kjeldahl nitrogen (TKN) and total nitrate nitrogen (TNN)), total suspended solids (TSS), total inorganic suspended solids (TISS), and planktonic chlorophyll *a* corrected for phaeopigments (CHL*a*). Temperature, pH, dissolved oxygen, and conductivity were measured with an H2O® Hydrolab. Turbidity readings were taken using a portable Hach turbidimeter (model 2100P).

Sediment samples were collected using either an Ekman grab sampler or a 5-cm Plexiglas tube with plunger and analyzed to determine the proportion of inorganic matter ($INORG_{SED}$) and total phosphorus (TP_{SED}) in the sediment (Crosbie and Chow-Fraser 1999). The maximum and dominant grain size in each sediment sample (20–70 g dry sediment) was classified according to the Wentworth scale (Wotton 1990); wetlands visited by Crosbie and Chow-Fraser (1999) were not analyzed for sediment size ($n = 22$).

We counted every species of submergent, emergent, and floating-leaf vegetation encountered within a 3-m radius of the selected vegetated site. In wetlands where submergent plant distribution was sparse (estimated as <5 plants·m^{-2}), we conducted an expanded survey along approximately 100 m of shoreline. Keys by Fassett (1940) and Newmaster et al. (1997) were used to identify the macrophyte specimens to species where possible. Because many wetlands were visited only once, and because certain species are difficult to identify accurately without flowering parts, many taxa were identified to genus only. Most submergent taxa were identified to genus, except for several common species that were keyed to species. All emergent taxa encountered were identified at

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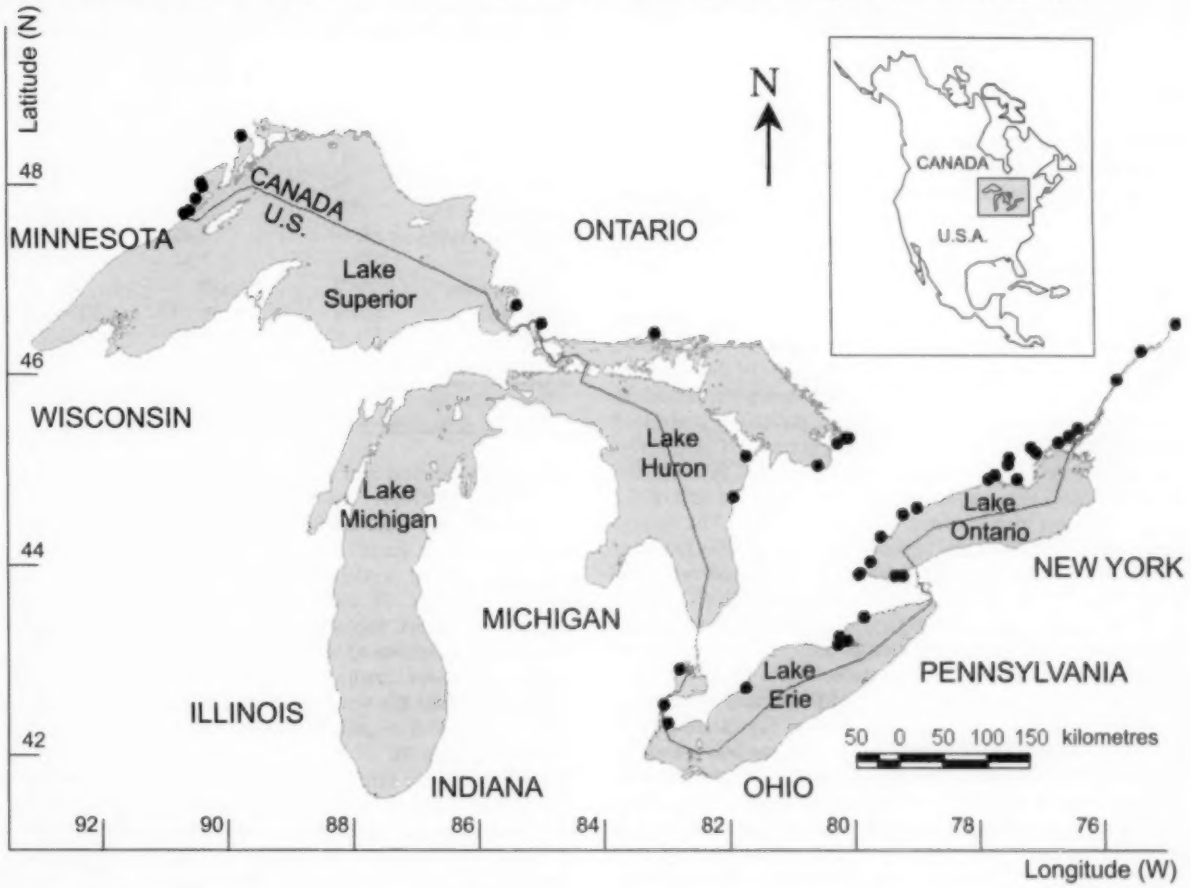
Fig. 1. Map of the Great Lakes of North America showing the location of the 62 wetlands sampled between 1995 and 1999.



least to genus, and the dominant taxa were noted. The objective of this plant survey was not meant to be exhaustive but rather to obtain floristic information on common taxa in a structurally diverse plant community that would include emergent, submergent, and floating-leaf components. Consequently, we did not sample along parallel transects of a systematic grid, an approach employed in studies designed to produce comprehensive species lists (e.g., Minc 1997; Magee et al. 1999). Our approach therefore likely excluded rare species and many grasses, rushes, and sedges that would have been more common in wet meadow environments (e.g., Minc 1997).

Proportion of agricultural, urban, and forested land was determined as described in Crosbie and Chow-Fraser (1999); however, for the three largest watersheds (>1500 km^2), land use was estimated from Detenbeck et al. (1999) (Goulais and Spanish River) and the Grand River Conservation Authority (Cambridge, Ont.; www.grandriver.on.ca). Wetlands were classified into land use categories as follows: (*i*) wetlands were assigned to the dominant land use category if the majority (>50%) of their watershed was of that land use and if <30% of the remaining catchment area was of another land use, (*ii*) wetlands were assigned to a combined land use category (e.g., agriculture/forested) if no land use type accounted for >50% of the total catchment area and the difference between any two types was <20%, and (*iii*) wetlands that occurred as fringes along the Great Lakes shoreline and did not have any obvious inflows were not classified to any land use ($n = 11$).

All statistical analyses were performed using SAS.Jmp software (SAS Institute Inc., Cary, N.C.), except for canonical correspondence analysis (CCA), which was performed using CANOCO version 4.0 (ter Braak and Smilauer 1998). Principal components analysis (PCA) was used to create linear combinations of the environmental data to describe the underlying environmental gradients in the data. Environmental data were $\log_{10}$ transformed (excluding pH) to approximate normal distributions and standardized to zero mean and unit variance. CCA was used to determine the best environmental factors to describe aquatic macrophyte distribution and has been used in similar studies relating macrophytes to their environment (e.g., Toivonen and Huttunen 1995; Bini et al. 1999; Magee et al. 1999). CCA maximizes the separation of species optima along synthetic axes, which represent linear combinations of environmental variables. CCA was appropriate in this study because the gradient lengths obtained from detrended correspondence analysis (CANOCO 4.0) indicated that the species data were moderately unimodal (ter Braak and Smilauer 1998).

Variables entered into the CCA included the presence of macrophyte taxa encountered in >10% of wetlands as well as accompanying environmental variables (i.e., TP, TN, TSS, CHL*a*, pH, conductivity (COND), TP_{SED}, $INORG_{SED}$, latitude (LATITUDE) (in decimal degrees)). We excluded turbidity, SRP, TISS, TKN, and TNN from the CCA because they showed a high degree of collinearity with chosen variables ($r > 0.90$) and contributed less to explaining the variation in the data set. All included variables had variance inflation factors <20, indicating that they contributed uniquely to the analysis (ter Braak and Smilauer 1998). The statis-

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tical significance of the relationship between the species data and environmental gradients was determined using Monte Carlo permutations (199 random permutations) (ter Braak and Smilauer 1998).

Results

Water and sediment quality

Wetlands in this study correspond to a wide range of environmental conditions, ranging from very clear and nutrient poor (e.g., TP = 16.3 $\mu g \cdot L^{-1}$, TN = 920 $\mu g \cdot L^{-1}$, CHL*a* ≥ 0 $\mu g \cdot L^{-1}$, TSS = 3.4 $mg \cdot L^{-1}$) to turbid and hypereutrophic (e.g., TP = 670 $\mu g \cdot L^{-1}$, TN = 9164 $\mu g \cdot L^{-1}$, CHL*a* = 239 $\mu g \cdot L^{-1}$, TSS = 209 $mg \cdot L^{-1}$) (Table 1). PCA was initially used to determine which environmental variables explained the greatest amount of variation in the data set (Table 2). The first three axes explained 72% of the variation in the data (Table 2), with nearly 50% being explained by PC axis 1. This axis was highly and positively correlated with variables associated with nutrient status (TN, TP, TNN) and particulate content (TSS, TISS, turbidity, CHL*a*) of the water. Conductivity, an indication of the ionic strength of the water, was also highly correlated with this axis. The second axis explained 16% of the variance and was positively correlated with $INORG_{SED}$ and negatively correlated with the phosphorus in the sediment. Wetlands with high PC axis 2 scores also had relatively high pH. PC axis 3, which explained only 10% of the variation in the data, was positively correlated with SRP and temperature.

Since PC axis 1 is associated with a nutrient–turbidity gradient, wetlands to the extreme right in Fig. 2 are turbid, hypereutrophic marshes, whereas those to the left are clear, nutrient-poor marshes. The majority of turbid, nutrient-rich wetlands in our data set are coastal wetlands of the lower Great Lakes, while clear, nutrient-poor wetlands correspond to inland wetlands and coastal wetlands of the upper Great Lakes. The second PC axis, which separates wetlands with largely organic, fertile sediment and low pH from those with inorganic, infertile sediment and high pH, is a good discriminator for inland and upper coastal wetlands. Coastal wetlands in the upper lakes (Huron, Superior) tend to have a higher pH and a greater proportion of $INORG_{SED}$ (analysis of variance (ANOVA), Tukey–Kramer, $p < 0.05$), while inland wetlands tend to have more organic sediment and higher TP_{SED} (ANOVA, Tukey–Kramer, $p < 0.05$).

Land use

Given development patterns in the Great Lakes basin over the past century, it was not surprising that the proportion of agricultural ($r^2 = 0.50$, $p < 0.0001$) and urban ($r^2 = 0.08$, $p < 0.05$) land in wetland watersheds decreased significantly with latitude, while the proportion of forested land increased ($r^2 = 0.72$, $p < 0.001$). To determine the effect of land use on water and sediment quality, we regressed PC axis 1 scores against the proportion of the three different land use categories. PC axis 1 scores were positively related to percent agricultural land ($r^2 = 0.39$) (Fig. 3*a*) and negatively correlated with percent forested land ($r^2 = 0.40$) (Fig. 3*b*). Although we found no significant relationship between PC axis 1 scores and the proportion of urban land use, likely due to the small number of wetlands with >10% urban land in their watershed ($n = 6$), we found a significant regression when both percent agricultural and percent urban land were combined ($r^2 = 0.48$) (Fig. 3*c*).

Table 1. Range of environmental variables observed at 62 wetlands in the Great Lakes basin.

Variable	Mean	Range
TP ($\mu g \cdot L^{-1}$)	101	16.3–670
TN ($\mu g \cdot L^{-1}$)	2351	920–9164
TSS ($mg \cdot L^{-1}$)	23.3	3.4–209
Turbidity (NTU)	17.4	1.3–260
CHL*a* ($\mu g \cdot L^{-1}$)	20.2	0–239
Temperature (°C)	23.5	16.5–28.9
Dissolved oxygen ($mg \cdot L^{-1}$)	8.46	1.55–15
pH	7.54	6.0–8.7
COND ($\mu S \cdot cm^{-1}$)	388	39–1387
% $INORD_{SED}$	79.2	22.3–99.44
TP_{SED} ($mg \cdot g^{-1}$)	0.78	0.12–2.17
No. of submergent plant taxa	6	0–15

Note: CHL*a* determined from up to 500 mL of water filtered through GF/C filters. Zero values likely reflect insufficient sample volume.

The wetlands were further divided into three groups according to their location in the Great Lakes basin: inland wetlands, coastal wetlands of the lower Great Lakes, and coastal wetlands of the upper Great Lakes. For inland wetlands, land use explained a large amount of variation in PC axis 1 (indicative of water quality) and PC axis 2 (indicative of sediment quality). By contrast, land use was not as good a predictor for water quality in lower coastal wetlands and was not a significant predictor for upper coastal wetlands (Table 3).

Sediment grain size and organic content of the sediment also can be affected by land use as well as by geological factors and exposure. Because the PCA showed that sediment characteristics tended to vary by location, wetlands were again divided into the three groups according to their location. For inland wetlands, agricultural watersheds had a significantly higher proportion of $INORG_{SED}$ relative to forested watersheds (Wilcoxon rank sum, $p < 0.05$), while forested wetlands had a somewhat larger maximum sediment grain size (Wilcoxon rank sum, $p < 0.10$) (Table 4). There were no significant trends observed for the more exposed lower and upper coastal wetlands, where all wetlands contained significantly more inorganic soils relative to inland wetlands, especially in the upper lakes (ANOVA, Tukey–Kramer, $p < 0.05$).

Submergent plant species richness

The number of submergent plant species in the wetlands varied inversely with both PC axes 1 and 2 scores, although there was a great deal of scatter about the best-fit line ($r^2 = 0.32$ and 0.15, respectively) (Figs. 4*a* and 4*b*). A greater amount of the variation in the species richness data was explained by turbidity alone ($r^2 = 0.45$, $p < 0.0001$) (Fig. 4*c*). When data were sorted according to location, the percent variance explained by turbidity increased for inland ($r^2 = 0.67$, $p < 0.0001$) and lower ($r^2 = 0.54$, $p < 0.0001$) coastal wetlands but was not significant for upper lakes ($r^2 = 0.27$, $p = 0.0554$). Similarly, PC axis 2 explained 51% of the variance in species richness for inland wetlands but was not significant for either lower or upper wetlands. Figure 4 also

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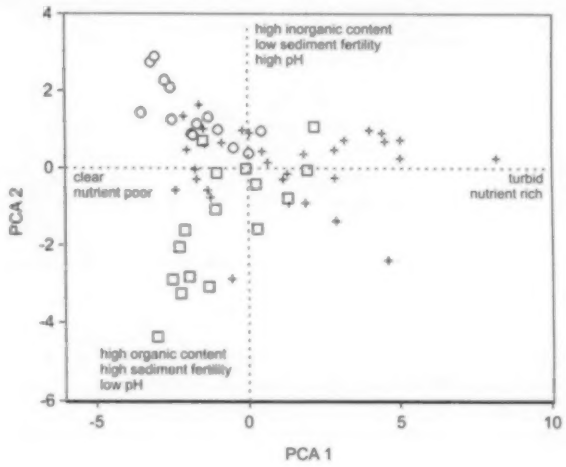
Table 2. Correlation coefficients between PC axes 1, 2, and 3 scores and environmental variables.

	Variance explained (%)	Environmental variable	*r*
PC axis 1	45.7	TSS	0.92
		Turbidity	0.89
		TN	0.88
		TP	0.87
		TISS	0.87
		CHL*a*	0.83
		COND	0.76
		TNN	0.71
PC axis 2	15.8	TP_{SED}	–0.85
		% $INORG_{SED}$	0.78
		pH	0.68
PC axis 3	10.4	Temperature	0.68
		SRP	0.52

Fig. 2. Plot of PC axis 1 versus PC axis 2 scores including inland (□), lower coastal (+), and upper coastal (○) wetlands.



shows that there were generally fewer submergent species in upper compared with lower and inland wetlands with similar turbidity PC axis 1 or PC axis 2 scores.

Macrophyte community structure

Submergent taxa that occurred in >50% of the wetlands included *Ceratophyllum*, *Elodea*, *Myriophyllum*, *Potamogeton pectinatus*, *Potamogeton richardsonii*, and *Vallisneria*. *Typha*, *Scirpus*, and *Lythrum salicaria* were the most prevalent emergents; *Nymphaea* and *Nuphar* also occurred in at least half of the wetlands. As explained in the methods, these emergent species are only representative of the dominant forms encountered in these wetlands.

We performed a CCA to determine the association between environmental variables and the distribution of macrophytes (Fig. 5). Sixty-two percent of the variation in macrophyte distribution could be explained by the first two synthetic environmental gradients. The most important predictors of macrophyte distribution, as indicated by their correlation with CCA axis 1, were TSS (r = 0.79), TP (r = 0.73), CHL*a* (r = 0.70), TN (r = 0.65), and COND (r = 0.61) (Fig. 5*a*). The second CCA axis was correlated with variables indicative of sediment quality (TP_{SED} (r = –0.54), $INORG_{SED}$ (r = 0.34), pH (r = 0.41)), although the strength of these correlations was weaker than that for CCA axis 1 scores. Not surprisingly, these variables were also the primary descriptors of the PC axes and those describing most of the variation in the submerged macrophyte species richness data. LATITUDE was moderately correlated with both CCA axes 1 (r = –0.38) and 2 (r = 0.38) and therefore confirms the distinction between higher latitude sites (clearer water, less nutrient- and organic-rich sediment) and lower latitude marshes (more turbid water, nutrient-rich, higher organic content sediment).

Location of plant taxa to the right of the origin in the biplot suggests that these plants tolerate a turbid, nutrient-rich water column (Fig. 5*a*). These included the emergent taxa *Typha*, *Sagittaria*, and *Lythrum*, submergent taxa *Potamogeton pectinatus* and *Potamogeton crispus*, and the floating taxa *Nuphar variegatum* and *Nymphaea odorata*. Those taxa that were least tolerant of turbidity and eutrophication included the emergent taxa *Pontederia cordata* and *Sparganium* sp., the majority of the submergent taxa (e.g., *Potamogeton richardsonii*, *Najas flexilis*, *Utricularia* sp.), and the floating-leaf species *Potamogeton natans*. Submergent taxa that were moderately tolerant of turbid water included *Elodea canadensis* and *Ceratophyllum demersum*. Taxa more influenced by CCA axis 2 and common in more inorganic, infertile soils at higher latitudes included *Scirpus* sp. and *Potamogeton richardsonii*. Several taxa were excluded from the CCA because of their rare occurrence, and some of these taxa displayed obvious trends in their distribution. Most notably, *Potamogeton gramineus*, *Eleocharis smallii*, *Isoetes* sp., and *Zizania palustris* were found north of 44° latitude in wetlands with relatively low water turbidity and nutrient concentrations.

Figure 5*b* displays the location of the site scores for the CCA analysis. In general, CCA axis 1 separates the turbid, nutrient-rich wetlands in highly agricultural and urban watersheds from the clearer, more oligotrophic wetlands located in moderately to largely forested watersheds. CCA axis 2 separates higher latitude forested sites from all other sites. Three main macrophyte community types are apparent. In the upper left quadrant of the CCA biplot are higher latitude sites in forested watersheds where the emergent vegetation is often dominated by *Scirpus* sp., *Eleocharis smallii*, *Potamogeton gramineus*, and *Potamogeton richardsonii*. The mean number of submergent taxa found in these wetlands was 6.5, and one quarter of the wetlands in this quadrant had a low stem density of submergents (<5 stems·m^{-2}). By contrast, *Typha* was the dominant emergent in the lower latitude sites, which are plotted in the lower half of the biplot. Wetlands located in the lower left quadrant correspond to relatively high-quality wetlands in forested watersheds with relatively high species richness of submergent taxa (mean = 10.3 species) where the submergents formed dense mats (all wetlands >5 stems·m^{-2}). Wetlands located on the right-hand side of the biplot, however, correspond to turbid, nutrient-rich wetlands with highly developed watersheds. These contain relatively few submergent taxa (mean = 3.6 taxa), with

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Fig. 3. PC axis 1 scores against arcsine-transformed percent (*a*) agricultural land, (*b*) forested land, and (*c*) agricultural and urban land.

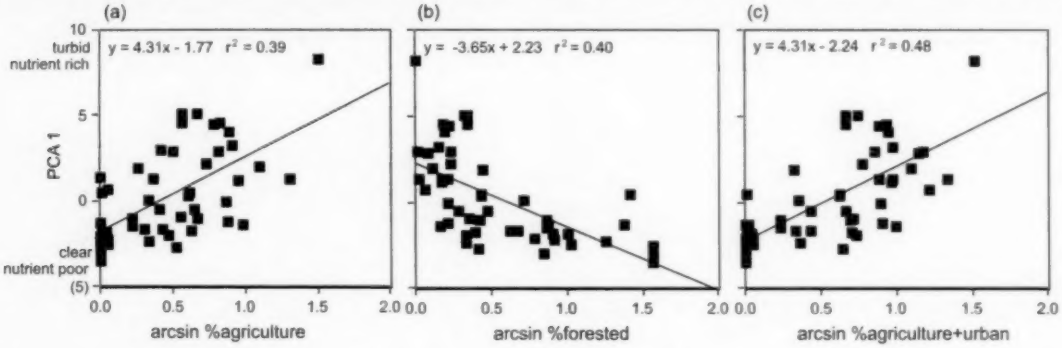

Table 3. Characteristics of the regression relating land use (agricultural, agricultural and urban, forested) in each region (inland, lower coastal, upper coastal) to PCA axes 1 and 2.

		PCA axis 1		PCA axis 2	
		r^2	p	r^2	p
% agricultural	Inland	0.67	0.0003	0.34	0.0284
	Lower	0.16	0.0489	—	—
	Upper	—	—	—	—
% agricultural and urban	Inland	0.61	0.0009	0.29	0.0457
	Lower	0.22	0.0181	—	—
	Upper	—	—	—	—
% forested	Inland	0.60	0.0012	0.23	0.08
	Lower	0.16	0.0511	—	—
	Upper	—	—	—	—

45% of the wetlands containing a low stem density of submergents (<5 stems·m^{-2}) and only a fringe of *Typha*.

Discussion

The species richness and community structure of aquatic macrophytes in wetlands of the Great Lakes basin appeared to be a function of the geographic location of the wetland (i.e., whether they are associated with the upper or lower Great Lakes or located inland) and the degree of water quality degradation. For inland wetlands, the primary source of water quality degradation was excess inputs of nutrients and sediment associated with agricultural development in the watershed. For coastal wetlands, however, water quality may have also been influenced by mixing with water in the lake proper. In particular, wetlands in the less developed and more exposed upper Great Lakes had unique physical and ecological characteristics when compared with more developed and less exposed wetlands of the lower Great Lakes and inland locations.

The proportion of agricultural and urban land in wetland watersheds was a highly significant predictor of water quality (PC axis 1), explaining almost half of the variation in the dependent variables. These results are consistent with previous studies where water quality was related to land use in the watershed (Johnson et al. 1997; Crosbie and Chow-Fraser 1999). There was, however, a great deal of variability observed due to climatic and geological differences associated with different latitudes (upper versus lower lakes) and exposure (inland versus coastal). Water quality in inland wetlands was substantially degraded by urban and agricultural land use. Inland wetlands that received a disproportionate amount of agricultural runoff tended to have a greater proportion of fine, inorganic silts and clays in their sediment compared with those in mainly forested watersheds that have a deep layer of organic muck and larger gravels in their substrate (Minc 1997). The presence of high silt and clay content in the sediment is undesirable, since plants grow better in organic than in inorganic substrates (Day et al. 1988), and small inorganic particles in the sediment can become easily resuspended and stay in suspension (Hamilton and Mitchell 1997), thus keeping the water column turbid and light limited for macrophytes. Conversely, forested land appeared to attenuate the delivery of sediment from the watershed to inland wetlands and can apparently contribute to a greater level of organic matter in these wetlands.

It is noteworthy that land use effects were greatest on water and sediment quality in inland systems that do not have direct hydrological links with the Great Lakes. In coastal wetlands, the flow of water between the marsh and the Great Lake in question can be reversed depending on watershed inputs, wind direction, and water level (Chow-Fraser 1999; Botts 1999); hence, mixing with lake water may ameliorate the effects of upstream pollution, while wind and wave action in exposed coastal marshes may lead to export of organic matter from the wetland to the lake (Day et al. 1988). The geomorphological characteristics of the Canadian shorelines of the Great Lakes have produced largely exposed shorelines and lacustrine embayments along the upper lakes as compared with a large number of riverine-type wetlands and a smaller proportion of protected lacustrine embayments in Lakes Erie and Ontario (Smith et al. 1991; Chow-Fraser and Albert 1999). In our study, 70% of our upper lake wetlands and only 33% of the lower lake wetlands were classified as lacustrine. Consequently, intrusion by lake water and exposure to wave action may play an even larger role in affecting wetland water quality in the upper lakes than in the more protected wetlands of the lower lakes.

Many studies have shown that nutrient enrichment can cause substantial changes in the species richness, composition, and density of aquatic vegetation in lakes (e.g., Toivonen and Huttunen 1995; Bini et al. 1999; Magee et al. 1999). Our results confirm that submergent macrophyte biodiversity in Great Lakes wetlands declines with deterioration

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Fig. 4. Number of submersed plant taxa plotted against (*a*) PC axis 1 scores, (*b*) PC axis 2 scores, and (*c*) log turbidity (nephelometric turbidity units) including inland (□), lower coastal (+), and upper coastal (○) wetlands.

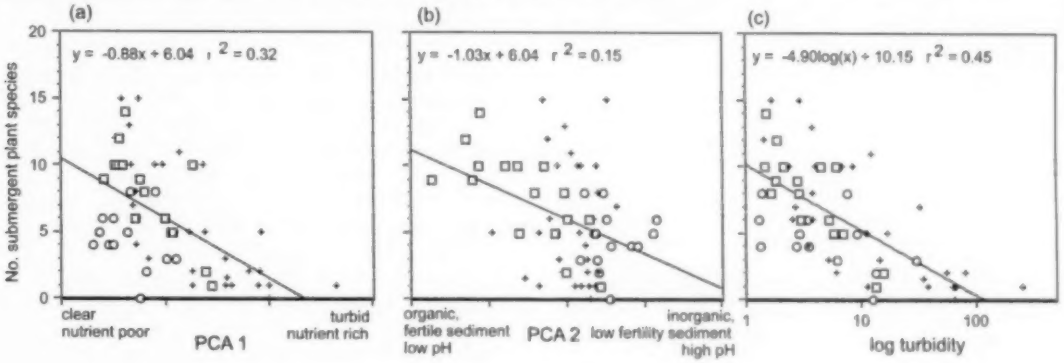

Table 4. Comparisons of means (and standard errors) of the percent organic composition of the sediment and the maximum sediment size observed in wetlands characterized by different land use types (agricultural, forested, agricultural/forested, urban) in inland, lower coastal, and upper coastal systems.

		n	% organic	Maximum sediment size (μm)
Inland	Agricultural	4	16.5 (4.3)*	0.156 (0.094)*
	Forest	8	49.8 (6.8)*	16 (0)*
	Agricultural/forested	2	76.1 (1.7)	0.0039 (0)
Lower	Agricultural	17	17.2 (4.3)	0.094 (1.98)
	Forest	2	23.9 (14.8)	8.03 (7.97)
	Agricultural/forested	2	21.8 (0.6)	0.25 (0)
	Urban	4	29.1 (11.4)	0.125 (0)
Upper	Agricultural	1	6.62 (0)	0.0625 (0)
	Forest	8	3.0 (0.8)	9 (2.91)
	Agricultural/forested	2	8.73 (7.58)	8.03 (7.97)

Note: Asterisks indicate significant differences among inland sites (Wilcoxon rank sum, $p < 0.05$).

in water quality. This is consistent with a study by Findlay and Houlahan (1997), who also found reduced species richness of both aquatic and terrestrial organisms with increasing development in wetland watersheds of southeastern Ontario. In particular, we found that 45% of the variation in submergent plant species richness could be explained by turbidity alone. The tolerance of aquatic macrophytes to reduced light availability is tightly linked to their structural characteristics. While emergent and floating-leaf macrophytes are not generally affected by light availability (Day et al. 1988; Toivonen and Huttunen 1995; Bini et al. 1999), submergents tend to be greatly influenced by reduced water clarity. Our results confirm that submerged macrophytes that are canopy-formers such as *Potamogeton pectinatus*, *Myriophyllum* sp., and *Ceratophyllum* are able to survive in situations of light limitation, as opposed to species such as *Chara* and other *Potamogeton* spp., whose leaves grow below the surface (Chambers and Kalff 1987; Minc 1997).

The synergistic effects of many factors including eutrophication and algal and nonalgal turbidity (Phillips et al. 1978) and sediment characteristics (Carignan and Kalff 1980; Barko and Smart 1983; Day et al. 1988) can all affect macrophyte growth. Because of their sensitivity to this large suite of physical and chemical variables, many macrophyte taxa have been used as indicators of trophic state in other systems (e.g., Grasmück et al. 1995; Thiébaut and Muller 1998). In this study, there appears to be certain taxa that are intolerant of turbid, nutrient-rich conditions (e.g., *Pontederia cordata*, *Potamogeton richardsonii*, *Najas flexilis*, *Utricularia* sp.) but none that occur exclusively in degraded sites. Although some taxa appear to be more tolerant of water and sediment quality degradation (e.g., *Typha*, *Sagittaria*, *Potamogeton pectinatus*, *Nuphar*, *Nymphaea*), including exotic species such as purple loosestrife (*Lythrum salicaria*) and curly-leaf pondweed (*Potamogeton crispus*), even these taxa can be found in high-quality wetlands that are not turbid and eutrophic. What appears to be a better indicator of wetland quality is the type of community present rather than the presence of certain indicator species. The presence of a fringe emergent community with only a few sparsely distributed submergent taxa is highly indicative of a turbid, nutrient-rich wetland, whereas a mix of emergent and floating-leaf taxa with a diverse and dense submergent community is highly indicative of a high-quality wetland.

Species richness and plant density tend to be low in oligotrophic systems. As nutrient concentrations increase in these impoverished systems, both the stem density and the diversity of macrophytes increase until such time as light becomes limiting and plant abundance starts to level off (Lachavanne 1985; Toivonen and Huttunen 1995). The most oligotrophic sites in this study tended to be associated with the upper lakes, where species richness and density were substantially lower than in the lower lakes; however, inland wetlands of similar trophic state showed greater species richness and plant density. In the Great Lakes basin, the relationship between water quality and the macrophyte community is definitely confounded by the strong latitudinal gradient that exists from the southern- to northernmost points (Smith et al. 1991). The macrophyte communities in the upper and lower lakes differed substantially in their dominant species. In lower latitudes, emergent marshes tended to be dominated by *Typha* sp., while in the upper lakes the dominant emergent tended to be *Scirpus* sp. or *Eleocharis smallii*. There were fewer submergent taxa overall in the upper lakes, with the most frequently observed being relatively sparse beds of *Potamogeton gramineus*, *Potamogeton richardsonii*, and

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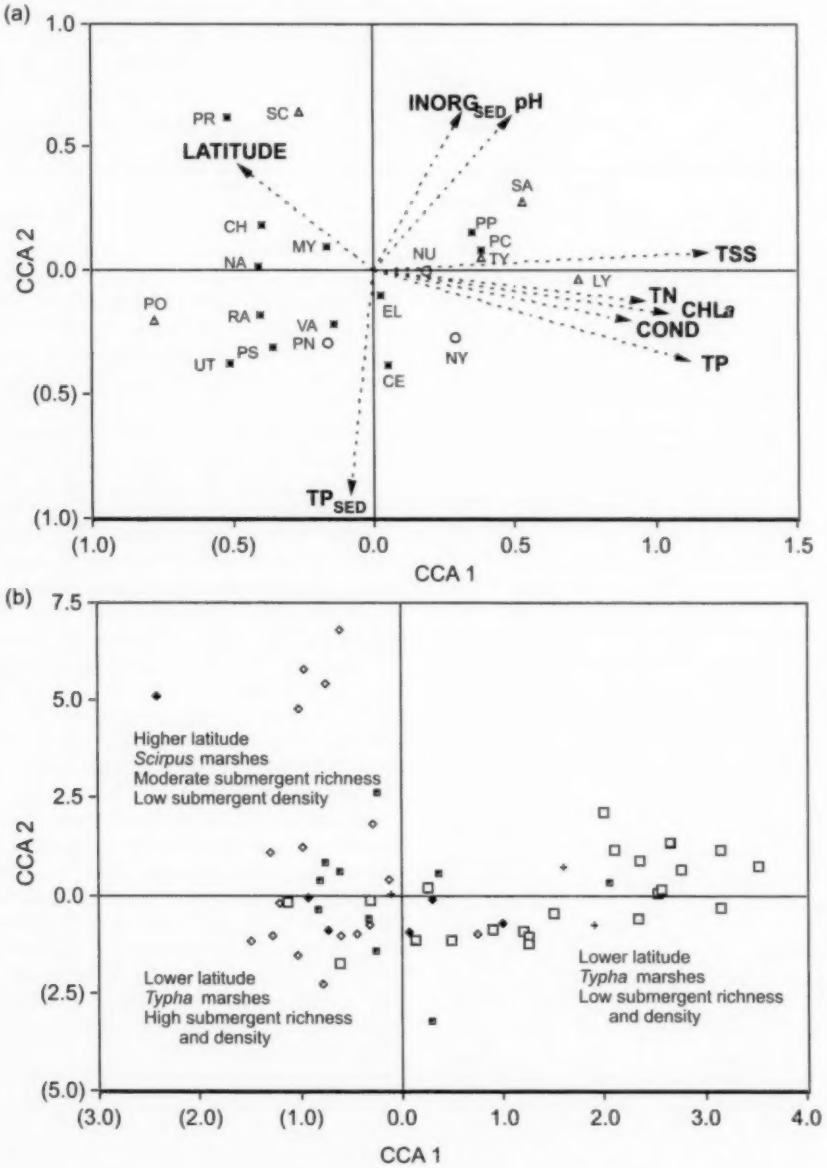
Fig. 5. Biplot of the CCA. (*a*) Environmental vectors and common macrophyte species (occurred in >10% of the wetlands sampled): submergent (■), emergent (△), and floating (○); (*b*) location of site scores classified into land use categories: agricultural (□), forested (◇), agricultural/forested (◆), urban (+), and unknown (■). Submergent species: *Ceratophyllum demersum* (DE), *Chara* sp. (CH), *Elodea Canadensis* (EL), *Myriophyllum* sp. (MY), *Najas flexilis* (NA), *Potamogeton* sp. (PS), *Potamogeton crispus* (PC), *Potamogeton pectinatus* (PP), *Potamogeton richarsonii* (PR), *Ranunculus* sp. (RA), *Utricularia* sp. (UT), *Vallisneria americana* (VA). Emergent species: *Lythrum salicaria* (LY), *Pontederia cordata* (PO), *Sagittaria latifolia* (SA), *Scirpus* sp. (SC), *Typha* sp. (TY). Floating-leaf species: *Nuphar variegatum* (NU), *Nymphaea odorata* (NY), *Potamogeton natans* (PN).



Isoetes sp. Conversely, there was a more diverse, dense, and variable submergent plant community in the high-quality wetlands of the lower lakes and fewer submergent species present in more turbid, sparsely vegetated wetlands.

The importance of latitude in structuring the macrophyte community in the Great Lakes basin is due to several factors, including climate and geology (Smith et al. 1991; Minc 1997). A strong latitudinal gradient exists between the upper and lower lakes, which affects the length of the growing season and the annual input of solar radiation. Furthermore, the soft sedimentary rock underlying the lower lakes provides expansive areas of shallow water and fine-textured sub-

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strates favorable for marsh development, while the older igneous and metamorphic bedrock in Lake Superior and Georgian Bay (Lake Huron) results in a deeper and more exposed shoreline with large-textured inorganic substrates. Plants grow best in organically rich and fertile substrates (Barko and Smart 1983), which are generally lacking in the upper lakes. Consequently, we saw sparse vegetative communities consisting of species better adapted to the shorter growing season and lower substrate fertility of the northern lakes such as *Scirpus*, *Eleocharis*, *Equisetum*, *Potamogeton gramineus*, and *Isoetes* (Day et al. 1988; Minc 1997). These taxa were largely absent from the lower lakes and were replaced by taxa more indicative of a southern community such as *Ceratophyllum* (Minc 1997).

In conclusion, as has been observed in several other large-scale studies (Smith et al. 1991; Minc 1997), physical factors largely related to geology and latitude such as exposure, sediment composition, and length of growing season may be important determinants of macrophyte community composition in coastal wetlands of the Great Lakes. In lower coastal and inland wetlands, plants are distributed according to a nutrient and clarity gradient, which was inextricably linked to land use in the watershed. In coastal lacustrine wetlands, especially in the upper lakes, land use plays less of a role in affecting water and sediment quality than mixing with the lake proper. Because aquatic plants are tightly linked to the functional capacity of wetlands, providing habitat and a sink for sediment and nutrients, the cumulative impacts of altered land use may reduce these important wetland values. We echo the management challenge issued to all levels of government at the State of the Lake Ecosystem Conference (e.g., Bertram and Statler-Salt 1999) to promote land use that is both efficient and protective of high-value nearshore habitat in the Great Lakes.

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Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered

Caihong Fu, Robert Mohn, and L. Paul Fanning

Abstract: An age-structured population dynamics model, incorporating interactions between Atlantic cod (*Gadus morhua*), the fishery, and the grey seal (*Halichoerus grypus*) population, was applied to the cod stock off eastern Nova Scotia (Northwest Atlantic Fisheries Organization Divisions 4Vs and 4W, commonly abbreviated to 4VsW), a stock that has dramatically declined since the late 1980s. Mortality was modeled as having three components: fishing mortality (F), seal predation (M^p), and all other sources of natural mortality (M). Specifically, M was assumed to be distinct for immature cod (ages 1–4; M^i) and mature cod (age 5 and older; M^m), and respective annual variations were estimated. Parameters estimated also included recruitment (cod abundance at age 1; R), F, and M^p. Based on our estimates of F, M^p, and M, it is unlikely that the collapse of the 4VsW cod stock can be attributed to a sudden increase in M; fishing appears to have been the primary cause for the stock's decline. However, after the moratorium on commercial fishing in 1993, increasing M^p and M^m and low R may have contributed to the failure of the 4VsW cod stock to recover.

Résumé : Un modèle de dynamique de population basé sur les structures d'âges qui incorpore les interactions entre la Morue franche (*Gadus morhua*), les pêches commerciales et la population de Phoques gris (*Halichoerus grypus*) a été appliqué au stock de morues du large de la côte est de la Nouvelle-Écosse (divisions 4VsW de l'Organisation des pêches de l'Atlantique nord-ouest), un stock qui a chuté de façon dramatique depuis la fin des années 1980. La modélisation de la mortalité a trois composantes, la mortalité due à la pêche (F), la prédation par les phoques (M^p) et les autres sources de mortalité naturelle (M). Plus précisément, une mortalité distincte est attribuée aux morues immatures (âges 1–4, M^i) et matures (âges 5 et plus, M^m) et, pour chacune, les variations annuelles sont estimées. Les variables, comme le recrutement (R, abondance des morues à l'âge 1), F et M^p, sont aussi estimées. D'après nos estimations de F, M^p et M, il est peu probable que le déclin du stock 4VsW soit attribuable à une augmentation soudaine de M; les pêches commerciales semblent avoir été la cause principale de la chute du stock. Toutefois, après le moratoire sur les pêches commerciales en 1993, des valeurs croissantes de M^p et de M^m et un R faible peuvent avoir contribué à l'incapacité du stock 4VsW de se rétablir.

[Traduit par la Rédaction]

Introduction

Six Canadian stocks of Atlantic cod (*Gadus morhua*) ranging from southern Labrador to the continental shelf off eastern Nova Scotia collapsed almost simultaneously to the point where moratoria on commercial exploitation were declared in 1992 and 1993 (Myers et al. 1996). The reasons for these collapses were unknown, and were the subject of considerable debate. Some linked stock declines to natural causes and others to fishing activities. The ongoing debate over many other collapsed species across many jurisdictions underscores the difficulties of unambiguously demonstrating the relative influences of environmental, ecosystem, and fishing effects on heavily exploited species (Frank et al. 1996).

For the six cod stocks off eastern Canada, recruitment of year-classes that should have contributed most to the spawning stock at the time of collapses was found not to differ from recruitment levels in earlier years (Myers et al. 1997). High fishing mortality was identified as the primary cause for these collapses (Hutchings and Myers 1994; Myers and Cadigan 1995; Myers et al. 1996). On the other hand, Rose et al. (2000) argues that the collapses cannot be attributed in total to fisheries. Major environmental changes took place during the period of cod decline (Drinkwater and Mountain 1997), which may have led to the shift of cod distribution (Rose et al. 2000), reduced recruitment (deYoung and Rose 1993), and increased vulnerability to overfishing (Rose and Kulka 1999).

It was also suggested that body condition factors for cod in the northern Gulf of St. Lawrence declined throughout the early 1990s (Lambert and Dutil 1997), owing to poor environmental conditions (Dutil et al. 1999). The reduced condition of cod may have led to an increase in natural mortality, particularly for adults that have to invest energy reserves in reproduction (Lambert and Dutil 2000; Dutil and Lambert 2000). Diagnostic analysis of commercial catch and research-survey data obtained from the cod stock off southern

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Labrador and eastern Newfoundland suggested that large amounts of the 1987 year-class died as 4-year-olds in 1991 and as 5-year-olds in 1992 (Shelton and Lilly 2000). Although Myers and Cadigan (1995) rejected the hypothesis for the same cod stock that natural mortality increased in 1991, the increasing divergence of recruitment between research-survey analysis and virtual population analysis suggested increased losses of fish (Myers et al. 1997). Myers et al. (1997) attributed the losses to increased misreporting and discarding of catches of young. However, the quantity of missing fish in relation to the capacity of fishery at that time suggested that additional factors such as an increase in natural mortality due to reduced condition also played a role (Shelton and Lilly 2000). In addition, increased predation by seals may also have contributed to the collapse (Mohn and Bowen 1996).

In the case of each of the six collapsed cod stocks off eastern Canada, we may never be able to determine the relative importance of environmental changes (including predation) and fishing activities in the population changes. Nevertheless, there is little doubt that the sequential population analysis (SPA) which failed to provide acceptable population reconstruction during the time of population decline (Mohn 1999; Shelton and Lilly 2000) must have violated one or more of the model assumptions, such as constant natural mortality, accurate catch data, or constant research-survey catchability (Shelton and Lilly 2000). Thus, the most important question in stock assessment and fisheries management at this point is how to develop more realistic population models that require fewer and less rigid assumptions. This paper presents a modelling exercise intended to shed light on what may have happened to the cod stock off eastern Nova Scotia in Northwest Atlantic Fisheries Organization Divisions 4Vs and 4W (Fig. 1), commonly abbreviated to 4VsW.

The cod stock in 4VsW has been managed as one unit, although there is evidence that the cod stock in 4VsW comprises separate substocks (reviewed in Halliday and Pinhorn 1990). Before 1993, the stock was an important commercial resource. Catches averaged 49 600 (ranging from 10 000 to 80 000) metric tonnes (t) annually (Mohn et al. 1998). In 1992, the total catch reached 29 805 t under a total allowable catch (TAC) of 35 200 t. In 1993, the TAC was reduced to 11 000 t, in part because of the shortfall in 1992. Landings in 1993 amounted to 3474 t (Mohn et al. 1998), again considerably lower than the TAC. Population abundance of 4VsW cod appeared to have declined rapidly during 1993. The directed fishery for 4VsW cod was closed in September 1993, and abundance not only has remained low but has continued to decline since then.

Stock assessments of 4VsW cod have been undertaken routinely since 1975 (Halliday 1975). Stock assessments made before 1997 were based on SPA, assuming constant natural mortality of 0.2 over age and time (Fanning et al. 1996). However, there were concerns about the retrospective pattern in parameter estimates of population biomass and fishing mortality, i.e., the estimates deviated systematically as data were annually eliminated from or added to the assessment (Mohn 1999). Owing to the strong retrospective pattern, the most recent assessment was revised by assuming that natural mortality increased from 0.2 to 0.4 after 1985. In addition, predation by grey seals (*Halichoerus grypus*) was explicitly incorporated into the model because of increasing concern about removals attributed to seals (Mohn et al. 1998). These adjustments resulted in the retrospective pattern being greatly reduced, but its causes for the most part remained unknown. Also unresolved was what caused the population to decline, and whether consumption by seals had played an important role in cod population dynamics.

This paper develops a model based on a framework of interactions between cod, fisheries, and seals in which annual variations in natural mortality for both immature (ages 1–4) and mature cod (age 5 and older) were estimated explicitly. In addition, more parameter uncertainties were incorporated, including those in gear selectivity. The goal of this paper is to use this model to estimate time-varying mortality parameters and recruitment, to give a better rationale for the decline of the 4VsW cod stock and especially its failure to recover.

Methods

Data

Data used in the present work include catch at age from commercial fishery ($\tilde{C}_{t,a}$), exploitable number at age estimated from July research surveys ($\tilde{N}_{t,a}$), number at age consumed by grey seals ($\tilde{C}^{p}_{t,a}$) estimated according to Mohn and Bowen (1996), and cod weight at age estimated from commercial-fishery samples (W_a). Index t is for the years 1970–1997 and index a for ages from 1 to maximum age, A. The maximum age, A, was set at 12 to avoid many zeros in the data. There are two sets of estimated seal-consumption data, $\tilde{C}^{p}_{t,a}$, depending on the assumption of cod fraction in the diet of grey seals (Mohn and Bowen 1996). When the cod fraction in the seal diet is assumed to be constant, calculation of $\tilde{C}^{p}_{t,a}$ is independent of the size of the cod stock. If cod fraction is assumed to be proportional to cod-stock size, then the calculation of $\tilde{C}^{p}_{t,a}$ needs to be updated when the cod-stock size changes.

Population model

An age-structured separable model was constructed for the 4VsW cod stock. Because it is more convenient and easier to estimate a time series of parameters by estimating their deviations from a mean value (Otter Research Ltd. 1998), annual recruitment (R) at age 1 was modeled as $\ln(R_t) = \ln(\bar{R}) + \eta^{R}_{t}$, where $\bar{R}$ is the assumed average level set at 12 million and η^{R}_{t} is the deviation term. Similarly, instantaneous fishing mortality (F) of fully selected cod was modeled as $\ln(F_t) = \ln(\bar{F}) + \eta^{F}_{t}$ with $\bar{F}$ being set at 0.4. Cod age-classes were separated into two groups according to their maturity, following Mohn et al. (1998), where it was assumed that immature cod were aged 1–4 and mature cod were aged 5 and older. Natural mortality (M) was assumed to be distinct for immature cod (M^{i}) and mature cod (M^{m}). Mortalities M^{i} and M^{m} and predation mortality (M^{p}) were modeled as the time-series structure of a random walk: $\ln(M^{i}_{t+1}) = \ln(M^{i}_{t}) + \eta^{i}_{t}$, $\ln(M^{m}_{t+1}) = \ln(M^{m}_{t}) + \eta^{m}_{t}$, and $\ln(M^{p}_{t+1}) = \ln(M^{p}_{t}) + \eta^{p}_{t}$ where η^{i}_{t}, η^{m}_{t}, and η^{p}_{t} are the deviation terms.

Selectivity for the research-survey gear at age a was modeled as a logistic curve $s^{s}_{a} = \dfrac{1}{1 + e^{-\gamma^{s}(a-\delta^{s})}}$. Parameters γ^{s}, the shape parameter, and δ^{s}, the age at which 50% of the individuals are vulnerable to research-survey gear, were assumed to be time-independent. Gear selectivity for commercial fishing was modeled as three distinct logistic curves based on changes in the regulated trawl gear

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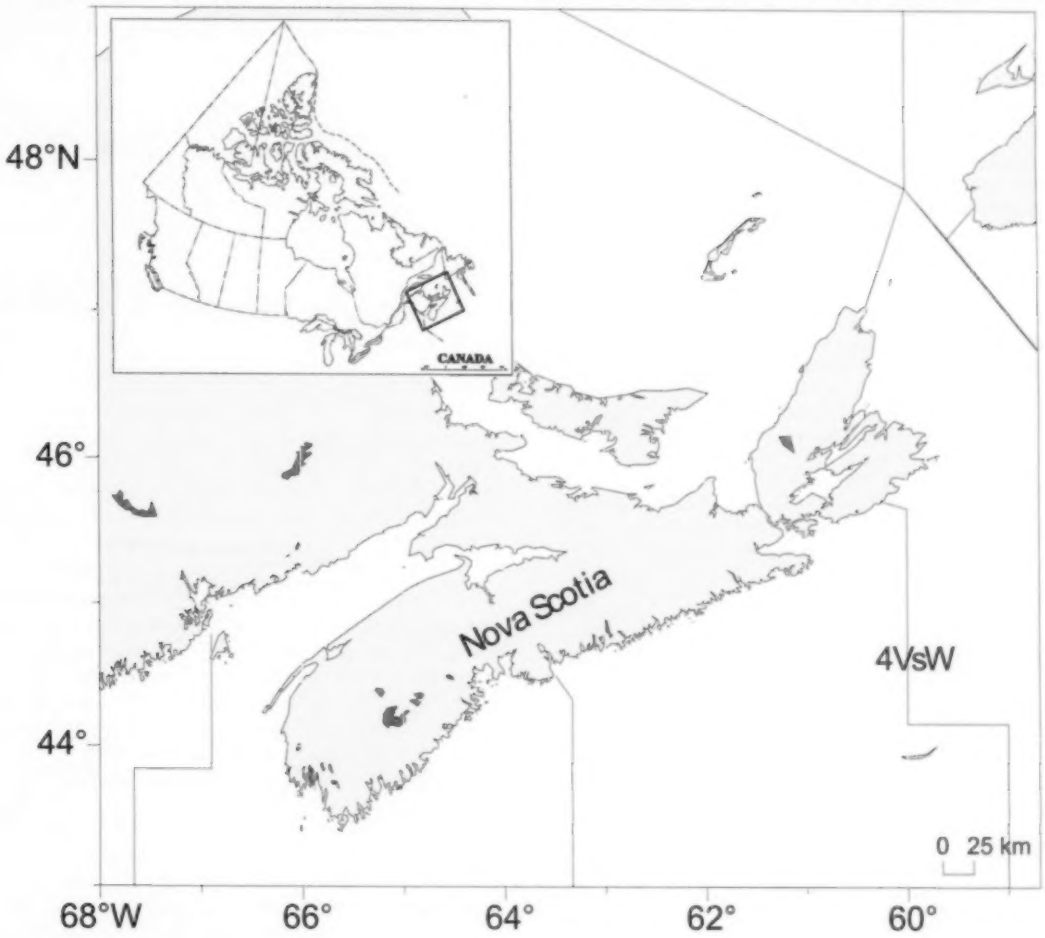
Fig. 1. Map showing the location of Northwest Atlantic Fisheries Organization Divisions 4VsW off eastern Nova Scotia, Canada.



mesh size over the fishing history: $s_a^{C_k} = \frac{1}{1 + e^{-\gamma^{C_k}(a-\delta^{C_k})}}$, with $k = 1$ for the period 1970–1976, $k = 2$ for 1977–1982, and $k = 3$ for 1983–1997. Predation selectivity was modeled as a descending logistic curve: $s_a^p = \frac{1}{1 + e^{\gamma^p(a-\delta^p)}}$ for ages 2–7. With age 1 cod, selectivity, s_1^p, was estimated individually to eliminate the pattern of consistently positive residuals of numbers of age 1 cod consumed. Predation selection, s_a^p, is assumed to be 0.0 for age 8 and older, based on seal-diet data.

The expected number of age 1 cod in year 1970 was calculated as $N_{1970,a} = \overline{R}e^{\eta_{1970}^R}$. For ages above 1, $N_{1970,a} = \overline{R}e^{\eta_{1970-a+1}^R} \prod_a e^{-M}$. Natural mortality during the initial period of $A - 1$ years before 1970, $\overline{M}$, was assumed to be constant at 0.2 because it has little effect on the estimation of other parameters (Fu and Quinn 2000). Expected numbers at age a in subsequent years are

$$N_{t,a} = N_{t-1,a-1}e^{-Z_{t-1,a-1}}, \quad 1 < a < A - 1,$$

and

$$N_{t,A} = N_{t-1,A-1}e^{-Z_{t-1,A-1}} + N_{t-1,A}e^{-Z_{t-1,A}}$$

Total mortality is $Z_{t,a} = F_t s_a^{C_k} + M_t^j + M_t^p s_a^p$, $a = 1,\ldots,4$, for immature cod and $Z_{t,a} = F_t s_a^{C_k} + M_t^m + M_t^p s_a^p$, $a = 5,\ldots,A$ for mature cod.

Expected numbers of catch at age follow the Baranov catch equation (Quinn and Deriso 1999): $C_{t,a} = N_{t,a}\frac{F_t s_a^{C_k}}{Z_{t,a}}(1 - e^{-Z_{t,a}})$.

Because of a change in research-vessel trawl gear in 1982 from Yankee 36 with width × vertical headline 11.0 × 3.4 m^2 to Western IIA with 12.5 × 4.6 m^2, survey catchability (q) was assumed to be different for the two periods. Thus, the expected numbers at age a for research surveys were calculated as $N_{t,a}^s = q_j N_{t,a} s_a^s$, where $j = 1$ for the period 1970–1981 and $j = 2$ for 1982–1997. Catchabilities q_1 and q_2 were arbitrarily set at 0.4 and 0.6, resepectively, the ratio of which is approximately the difference in net openings. Other levels were tried for evaluating sensitivity to their changes. Expected numbers of consumption at age a by grey seals in year t is

$$C_{t,a}^p = N_{t,a}\frac{M_t^p s_a^p}{Z_{t,a}}(1 - e^{-Z_{t,a}})$$

Parameters estimated include the time-dependent deviation terms η_t^R, η_t^F, η_t^p, η_t^j, and η^m. In addition, the following selectivity parameters for research survey, commercial fishing, and predation

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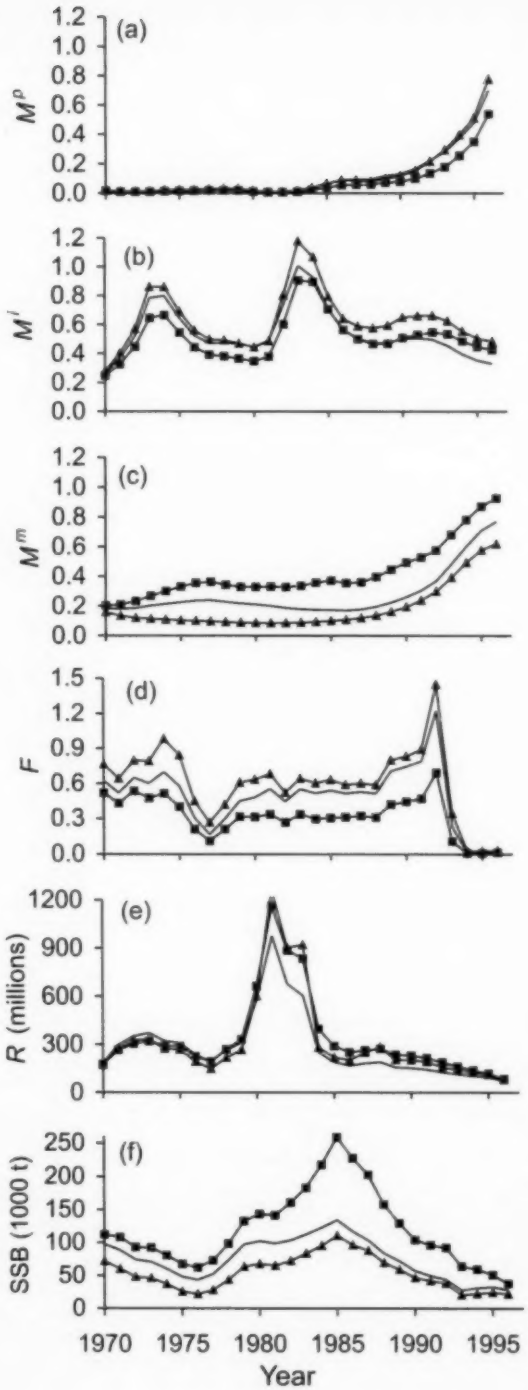

Fig. 2. Parameter estimates obtained using consumption data of constant cod fraction in seal diet under three assumptions of catchability (q): q_1 (before 1982) and q_2 (1982 and afterwards) are set at 0.4 and 0.6 (line without symbols), both at 0.3 (line with solid squares), and 0.8 (line with solid triangles), respectively. The estimates include predation mortality averaged over ages 1–4, M^p (*a*), natural mortality of immature cod, M^i (*b*), natural mortality of mature cod, M^m (*c*), instantaneous fishing mortality of fully recruited fish, F (*d*), recruitment, R (*e*), and spawning-stock biomass, SSB (*f*).

were estimated: γ^s, δ^s, γ^{C_k}, δ^{C_k}, s_1^p, γ^p, and δ^p. Parameter estimation was accomplished using the software AD Model Builder, which estimates parameters in a step-by-step fashion known as a multiphase procedure (Otter Research Ltd. 1998). A nonlinear least-squares (NLS) parameter-estimation procedure was applied. The NLS is robust to error structure in the data, such as in multinomial catch-at-age data, and could be expected to find parameter estimates more rapidly than the multinomial maximum likelihood method (Kimura 1990). Square-root transformation following Quinn et al. (1998) was used for all data. A logarithmic transformation was also applied and yielded quantitatively similar results, which are not presented. The following objective function is minimized for estimating parameters:

$$f = \lambda_C \sum_t \sum_a \left(\sqrt{\tilde{C}_{t,a}} - \sqrt{C_{t,a}} \right)^2 + \lambda_{N^s} \sum_t \sum_a \left(\sqrt{\tilde{N}_{t,a}} - \sqrt{N^s_{t,a}} \right)^2 + \lambda_{C^p} \sum_t \sum_a \left(\sqrt{\tilde{C}^p_{t,a}} - \sqrt{C^p_{t,a}} \right)^2 + \lambda_{M^i} \sum_t (\eta_t^{M^i})^2 + \lambda_{M^m} \sum (\eta_t^{M^m})^2$$

Weighting factors λ_C, λ_{N^s}, and λ_{C^p} were determined on the basis of the inverse of their residual variances and were set at 1.0, 0.3, and 1.0, respectively. In trials, parameter estimation was little affected by weighting factors of different data sources, which is consistent with the conclusion in Fu (2000). The terms $\lambda_{M^i} \sum (\eta_t^{M^i})^2$ and $\lambda_{M^m} \sum (\eta_t^{M^m})^2$ are penalties controlling the degree of variability in the time series of M^i and M^m estimates from year to year. The values of λ_{M^i} and λ_{M^m} are calculated as the product of $\tilde{N}_{t,a}$ residual variance, λ_{N^s}, an assumed coefficient of variation of $\tilde{N}_{t,a}$ (Fu and Quinn 2000), and the relative variation of M^i and M^m. We assigned 7500.0 and 5000.0 to λ_{M^i} and λ_{M^m}, respectively. The sensitivity of parameter estimation to the choice of λ_{M^i} and λ_{M^m} levels was examined.

Standard error and retrospective analysis

The bootstrap method (Efron and Tibshirani 1993) was used to estimate standard errors for the parameter estimates and predicted spawning stock biomass (SSB). Residuals from the original model were resampled. Parameter estimation was repeated 500 times using bootstrap data. Retrospective analysis (Mohn 1999) was conducted to evaluate the ability of the model to estimate parameters for the terminal years. This was done by reestimating parameters after leaving out successive terminal data with the full series, 1970–1997, which was eventually reduced to 1970–1983.

Results

Sensitivity to catchability

Survey data, $\tilde{N}_{t,a}$, are calibrated to the estimated population number at age using the catchability from research sur-

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veys. Fu (2000) demonstrates that q cannot be estimated with sufficient accuracy simultaneously with natural mortality (M), and it is better to keep q at a given level while estimating M each year even when there is variation in q (Fu and Quinn 2000). To examine how q affects the estimation of population parameters, we adopted various time-invariant levels of q and compared the parameter estimates and residual sum of squares (RSS). For purposes of the sensitivity evaluation, a constant fraction of cod in the seal diet is assumed to eliminate the nuisance effect of different $\tilde{C}^{p}_{t,a}$ values corresponding to different levels of q. In addition to the initially set q_1 and q_2 values of 0.4 and 0.6, alternative levels of 0.3 and 0.8 are also tried.

The estimation of M^p (shown as the average over ages 1–4), M^i, and R is robust to the assumed levels of q (Fig. 2). However, the estimated M^m, F, and SSB change dramatically in magnitude, with M^m and SSB decreasing and F increasing, when q increases from 0.3 to 0.8. The parameter estimates with q_1 and q_2 values of 0.4 and 0.6 are in between, and RSS is the lowest (Table 1*a*). The sensitivity evaluation suggests that the assumption concerning q is reasonable and will not affect the overall conclusions that we will draw hereinafter.

Sensitivity to consumption data

Because the estimated number at age consumed by grey seals, $\tilde{C}^{p}_{t,a}$, depends on the assumption made regarding cod fraction in the seal diet, it is necessary to explore predation scenarios (constant- and proportional-fraction sets of $\tilde{C}^{p}_{t,a}$) and examine how they affect the estimation of other parameters. In addition, we also estimate parameters after excluding the seal-consumption data to evaluate the performance of partition of M.

The estimates of M^m, F, and SSB are nearly identical under the three scenarios of seal consumption: (1) assuming a constant fraction, (2) assuming a proportional fraction, and (3) excluding the consumption data (Fig. 3). Assuming a constant fraction results in higher estimates of M^i (except for the last 2 years) and R. The R estimates from the third scenario (with consumption data excluded) are closer to those from the second scenario, which assumes a proportional fraction. Before 1983, when M^p was small, the M^i estimates from the third scenario are also closer to those from the second scenario. When the consumption data are excluded, the estimate of M^i rises gradually after 1988, reflecting the increase in M^p. The RSS from the second scenario (proportional fraction) is the lowest, and it increases drastically when the consumption data are excluded (Table 1*b*). In the following analyses, the data $\tilde{C}^{p}_{t,a}$ from the second scenario are used.

Sensitivity to penalty weighting

The estimates of M^i and M^m are closely related to the weighting factors λ_{M^i} and λ_{M^m} with higher levels resulting in reduced variations. Simulation studies indicate that appropriate weighting levels are related to measurement error in research-survey data (Fu 2000). We increased λ_{M^i} and λ_{M^m} by a factor of 3 from the originally assigned levels and then reduced them by factors of 3 and 6 to check sensitivity.

When the levels of λ_{M^i} and λ_{M^m} increase threefold, the estimates of M^i and M^m are nearly flat (Fig. 4). Recruitment

Fig. 3. Parameter estimates obtained using consumption data of constant fraction in seal diet (line with solid squares) and proportional fraction (line without symbols) and obtained with consumption data excluded (line with solid triangles). For details see Fig. 2.

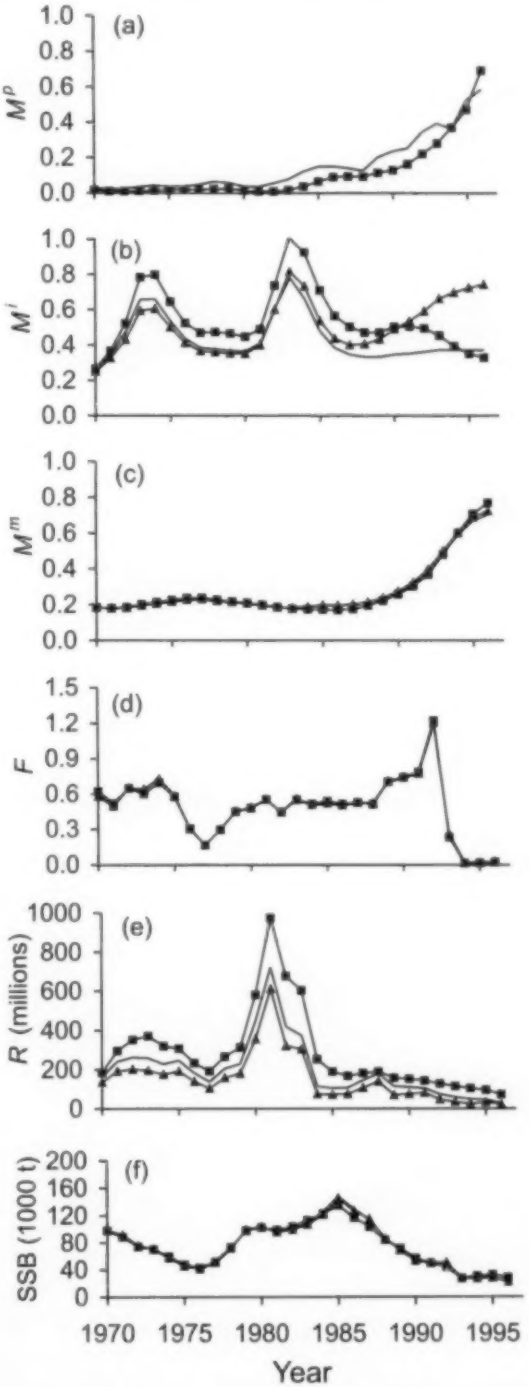

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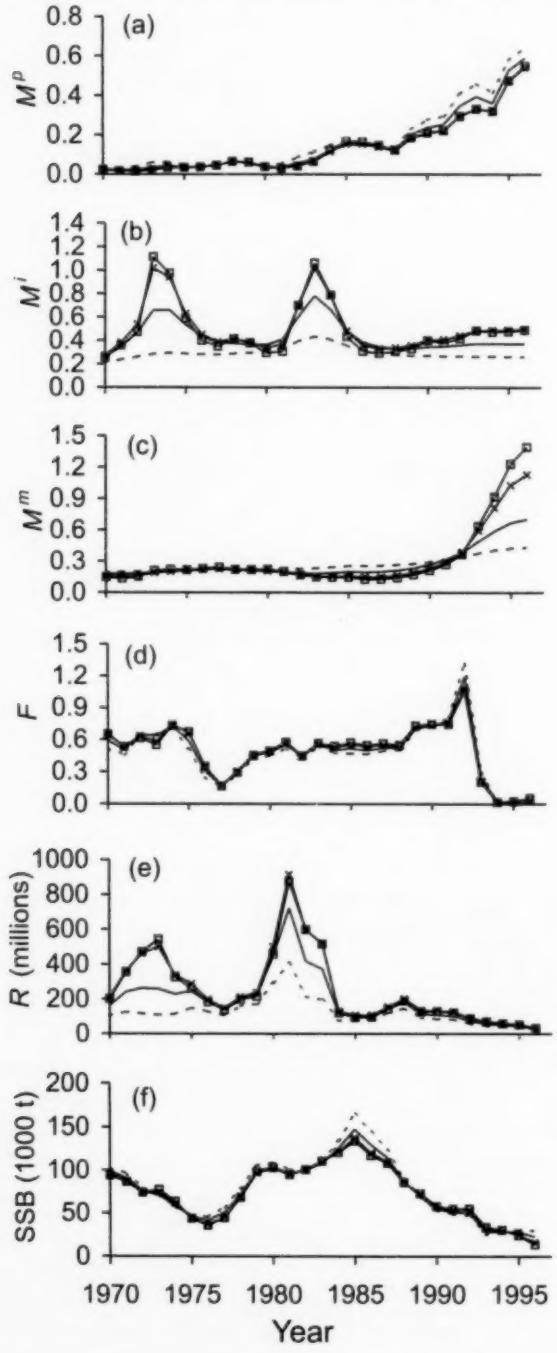
Fig. 4. Parameter estimates obtained using four sets of penalty weighting factors λ_{M^i} and λ_{M^m}: 7500 and 5000 (line without symbols), 3 times larger (broken line), 3 times smaller (line with ×), and 6 times smaller (line with open squares). For details see Fig. 2.



estimates decrease correspondingly and the RSS increases substantially. When the levels of λ_{M^i} and λ_{M^m} are reduced by a factor of 3, there are more dynamics in the estimates of M^i, M^m, and R; however, the overall time trend in the parameter estimates is not changed. Reducing λ_{M^i} and λ_{M^m} by a factor of 6 results in similar estimates of M^i and R, but much higher M^m, in the last 4 years. The RSS declines when the weighting factors are reduced (Table 1*c*), Although lower levels of the weighting factors are desired under low measurement errors with a resultant better fit to the data (Fu 2000), the uncertainty in the accuracy of the survey data led us to retain the intermediate levels.

Table 1. Residual sums of squares (RSS) from scenarios of sensitivity evaluation on catchability (*a*), seal consumption (*b*), and penalty weightings of natural mortality variability, λ_{M^i} and λ_{M^m} (*c*).

Catchability	Seal consumption	λ_{M^i} and λ_{M^m}	RSS
(*a*) Catchability			
0.3	Constant	7500, 5000	165 923
0.8	Constant	7500, 5000	188 198
0.4, 0.6	Constant	7500, 5000	162 467
(*b*) Seal consumption			
0.4, 0.6	Constant	7500, 5000	162 467
0.4, 0.6	Fraction	7500, 5000	157 010
0.4, 0.6	Excluded	7500, 5000	258 470
(c) Penalty weightings of natural mortality variability, λ_{M^i} and λ_{M^m}			
0.4, 0.6	Fraction	7500, 5000	162 467
0.4, 0.6	Fraction	2500, 1600	137 419
0.4, 0.6	Fraction	1250, 830	130 773
0.4, 0.6	Fraction	22500, 15000	185 962

Parameter estimation and standard error

Using catchability q_1 and q_2 of 0.4 and 0.6, respectively, the consumption scenario of proportional fraction, and the originally assigned penalty weighting factors for natural mortality deviations, we estimated the population parameters. Figure 5 shows the selectivity curves. Standard errors of the mortality parameters, R, and SSB were obtained from the bootstrap procedure (Fig. 6). The estimated M^p averaged over ages 1–4 has increased dramatically since 1988, and is nearly twice as large as M^i in the terminal year. The estimated M^i has two peaks, one in the early 1970s and another in the early 1980s, but has remained at a stable level since the mid-1980s. In contrast, the estimated M^m remains around 0.2 until 1990, after which it increases dramatically. The estimated F is around 0.7 in the 1970s, declines to 0.17 in 1977 at the time of extension of jurisdiction, and remains around 0.5 throughout the 1980s. Fishing mortality starts to climb in 1989 and peaks at 1.2 in 1992 before the fishery closure took place in 1993. The estimated R has one prominent peak in the early 1980s, and declines steadily after 1988. The estimated SSB declines steadily in the 1970s before starting to climb in 1977. SSB peaks in 1985, but declines steadily afterwards. Estimated total mortality from the model for both immature and mature cod agrees well, in general, with that directly calculated from the survey data (Fig. 7). However, survey data give much higher estimates of M^m for the last 3 years.

Retrospective analysis

Compared with previous results based on SPA (Mohn et al. 1998), retrospective analysis produces a much less severe

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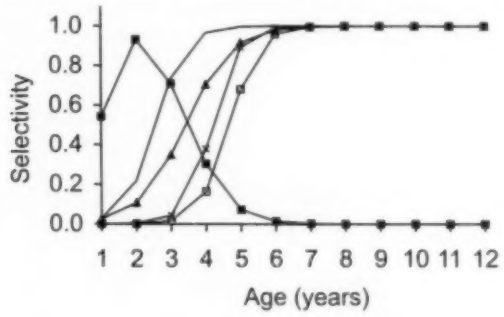
Fig. 5. Selectivity curves for predation (line with solid squares), survey gear (line without symbols), and commercial gear from 1970 to 1976 (line with solid triangles), from 1977 to 1982 (line with ×), and from 1983 to 1997 (line with open squares).



retrospective pattern in the estimates of all parameters except M^m (Fig. 8). The shape of the M^m estimates in the 1990s changes dramatically, from increasing to leveling out, when the last 2 years' data are removed. In addition, the estimates of M^i and R with data only up to 1984 deviate substantially from the values obtained from the analysis of the entire historical data series.

Discussion

This paper presents an age-structured model that uses multiple data sources from commercial-fishery, research-survey, and seal-diet analysis. This is the first stock-assessment study that estimates annual variations in natural mortality of both immature and mature cod. Our estimates of mortality indicate that except for the increase in F from 0.78 in 1991 to 1.2 in 1992, there is no dramatic increase in M^p, M^i, and M^m over the years 1991 and 1992. Our major conclusion is that the abrupt decline of the 4VsW cod stock in the early 1990s is unlikely to have been due to a sudden increase in M, and fishing appears to have been the primary cause.

The estimation of natural mortality indicates that M^i is more variable than M^m, which remains around 0.2 except in the last 4 years. Simulation studies indicate that M should be estimated annually when it varies over time (Fu and Quinn 2000). The variability in the M^i estimates suggests that M^i should be estimated each year as has been done here. When consumption data are excluded from the parameter-estimation procedure, the estimated M^i increases continuously after 1988, consistent with the increasing trend in the M^p estimates. This further suggests that estimating M^i annually is important, particularly when consumption data are unavailable. Estimating annual M^i captures mortality changes, whether they are due to predation or to other factors. Another major conclusion from this study is that estimates of M^p have increased dramatically since 1988 irrespective of the predation scenario. The consistency between the increasing trend in M^p and the difference between two series of M^i estimated with and without the consumption data indicates that partition of immature cod mortality into M^p and M^i is practical.

Sensitivity examination indicates that the estimate of M^i is robust to the assumption of q and primarily controlled by the weighting factor λ_{M^i}. Smaller measurement errors in survey data favor smaller weighting. However, if measurement er-

Fig. 6. Parameter estimates obtained using catchability q_1 and q_2 of 0.4 and 0.6, consumption data of proportional fraction in seal diet, and penalty weighting factors λ_{M^i} and λ_{M^m} of 7500 and 5000. For details see Fig. 2. Standard errors are shown as bar lines.

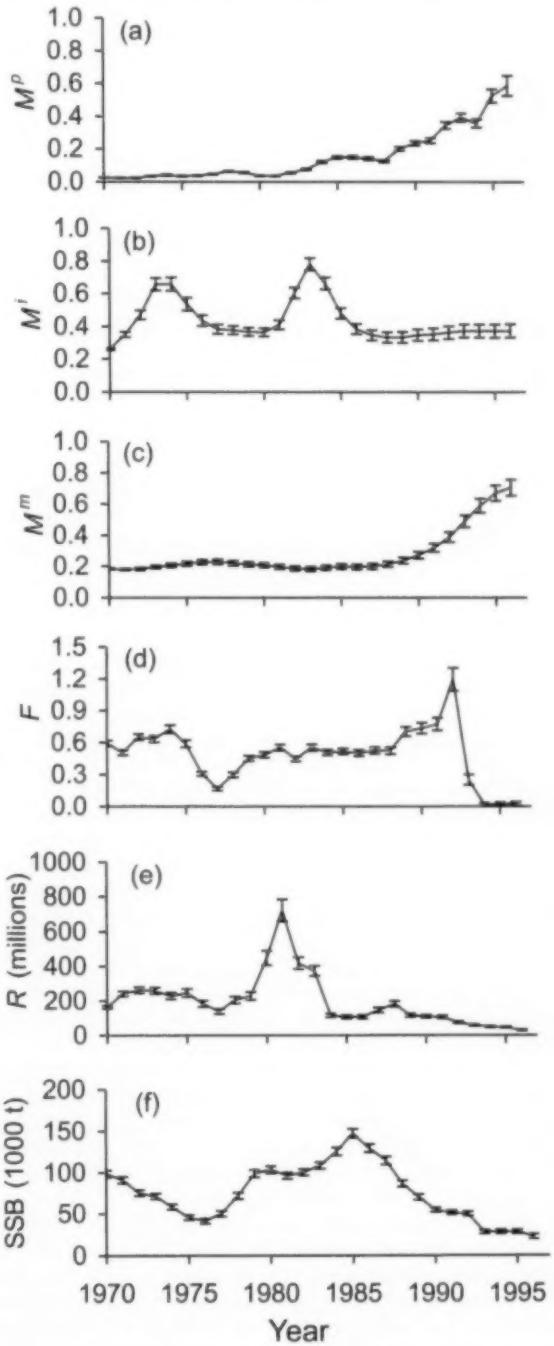


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Fig. 7. Total mortality (Z) estimated from the model (line) and solely from the survey data (solid triangles) for both immature cod (*a*) and mature cod (*b*).

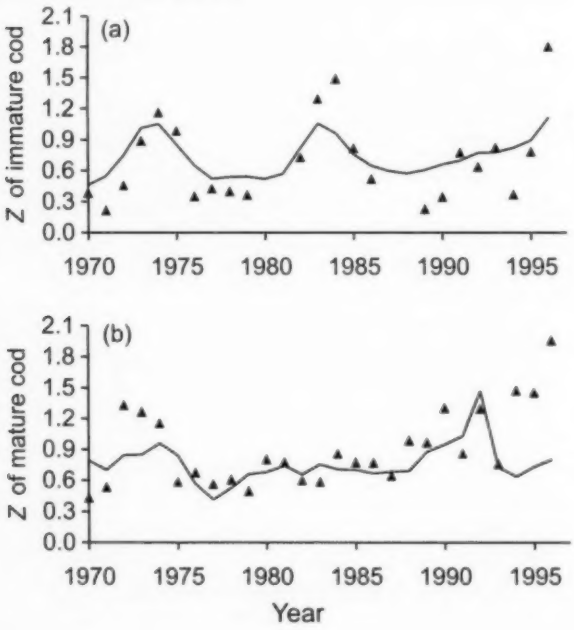
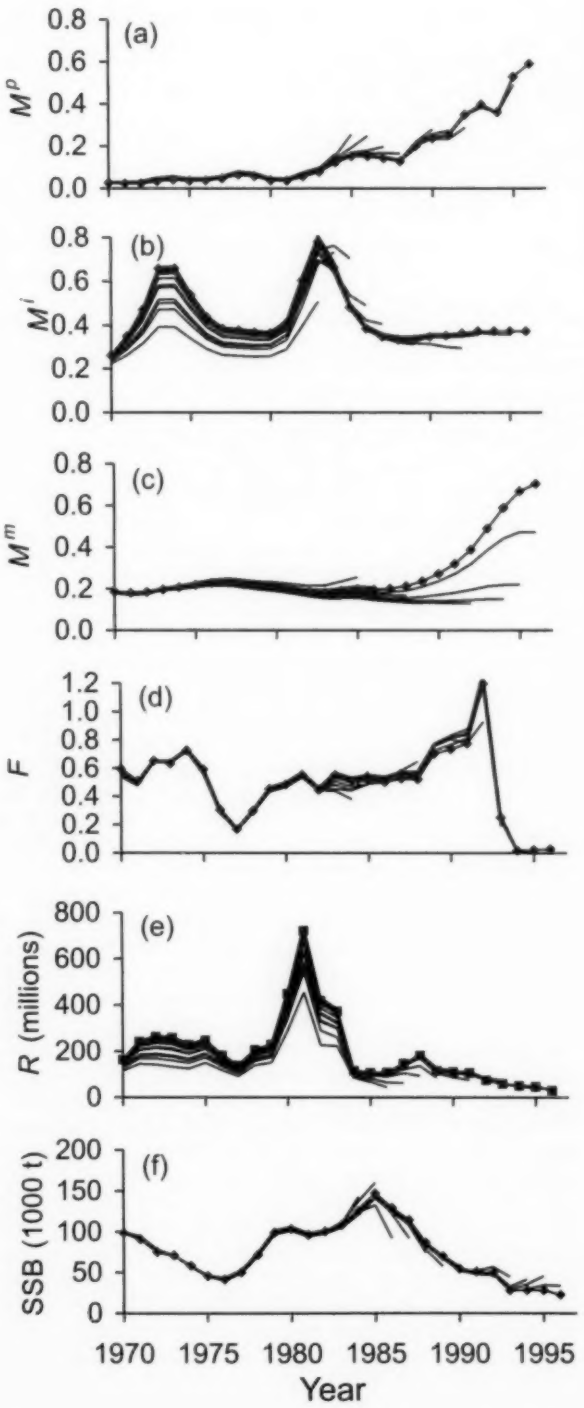


Fig. 8. Parameter estimates from retrospective analyses using data from 1970 to 1983 and all the way up to 1997. For details see Fig. 2.



rors are large and a small value is assigned to λ_{M^i}, then the M^i estimates can be overly sensitive to the errors in the survey data. On the other hand, if the measurement errors are lower than assumed, we run the risk of underestimating the magnitude and variability of M^i for the three periods of peaks in M^i: the early 1970s, early 1980s, and 1990s. Nevertheless, such an underestimation would not change our view of the stock status or our conclusions.

In contrast, the estimate of M^m is closely related to the q value. The higher q value, the lower the M^m estimates will be. Nevertheless, the time trend is not changed if the assumption of the overall q level is wrong. The estimates of M^m are rather stable before the decline of the stock in 1990s; however, they have increased by a factor of 3 over the last 7 years. It was noted that M^m was the only variable that displayed a severe retrospective pattern. Removing the last 2 years' data changes the shape of the M^m estimates completely. Further examination of the trend towards an increase in M^m estimates indicates that it is primarily caused by the low survey values of $\widetilde{N}_{t,a}$ in 1996 and 1997. Replacing these 2 years' data by those from 1995 gives a much slower increase in the M^m estimates.

Why did the survey estimates of mature cod abundance in 1996 and 1997 drop abruptly? The exact reasons are not known, but there are at least three possibilities. The first possibility is that the fish moved away and were unavailable to survey gear, as suggested by Rose et al. (2000) for the cod stocks off Newfoundland. However, this possibility is slim for the 4VsW cod stock because there is no evidence that cod abundance increased in other adjacent areas. The second possibility is that mature cod simply died, as the high M^m estimates suggest. Fishermen videotaped numerous carcasses

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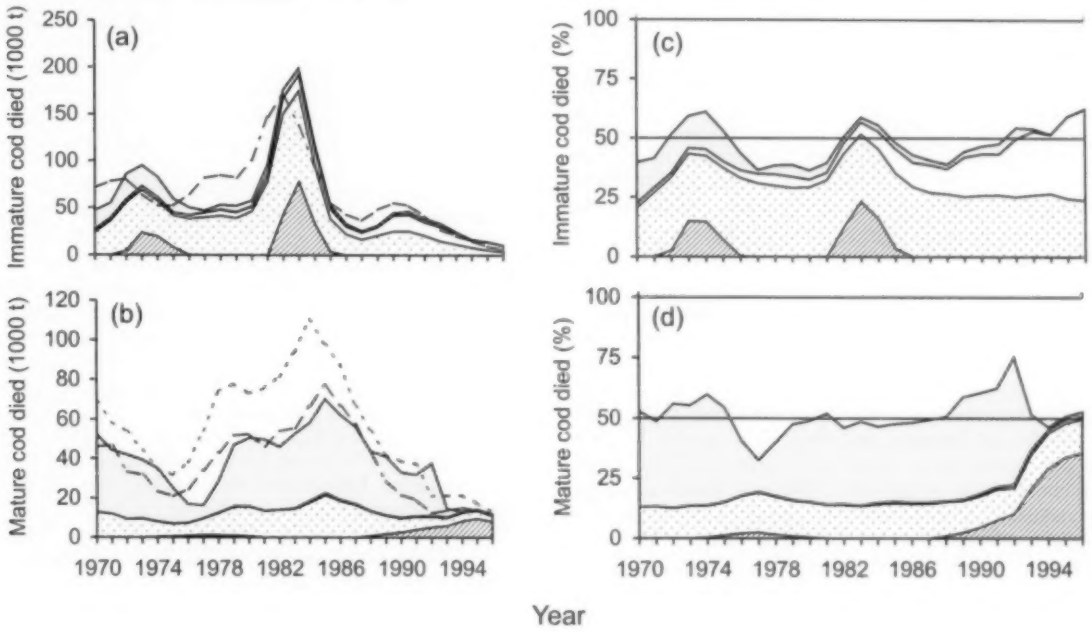
Fig. 9. (*a*) Comparisons among portions of immature cod biomass lost as a result of fishing mortality (grey-shaded area), predation mortality (open area), average immature-cod mortality, M^{i} (or M^{i} if it is less than the average) (dotted area), and the portion of M^{i} beyond its average (hatched area). The area below the broken line represents immature cod biomass that survived each year. (*b*) Comparisons among portions of mature cod biomass lost as a result of fishing mortality, predation mortality, 0.2 (or M^{m} if it is less than 0.2), and the portion of M^{m} beyond 0.2. The area below the lower broken line represents the mature cod biomass that survived each year, and that below the higher broken line represents the biomass of age 4 cod that survived each year. In *c* and *d*, biomass loss is shown as a percent for immature and mature cod, respectively.



of large cod left by seals that fed solely on the belly of these fish off Newfoundland, a form of predation not detectable by diet-estimation studies. The third possibility is that low recruitment throughout the early 1990s failed to replenish the mature cod stock. The low recruitment may have been due to environmental changes that reduced reproductive potential (Lambert and Dutil 2000); environmental changes are evident from the changes in species composition (Frank et al. 1996) and physical oceanography (Drinkwater and Mountain 1997). If the last two possible scenarios did occur, failure of the 4VsW cod stock to recover after the moratorium on commercial fishing would be expected.

Overall, the significant advance in our work is the relaxation of the assumption of a constant M, an assumption that can be easily violated (Fu 2000; Shelton and Lilly 2000). The estimation of annual variations in M leads to changes in the R estimates. Our R estimates are generally larger than those in Mohn et al. 1998, particularly for the early 1980s. Natural mortality and recruitment are positively correlated. When high M and high R values coexist, assessment models that assume a low constant M, such as 0.2, would underestimate the corresponding R. Thus, Mohn et al. (1998) appear to have systematically underestimated R. The extremely high R estimates from our model for the early 1980s are consistent with the research surveys that also reveal an extremely high R value in the early 1980s (Mohn et al. 1998). Overall, R estimates from assessment models of constant M could largely deviate from the true values if M, in fact, varies over time. Estimating annual variations in M is essential to a better understanding of the underlying population dynamics.

After the cod stocks off southern Labrador and eastern Newfoundland collapsed suddenly in 1992, it was hypothesized that M increased in 1991 (Myers and Cadigan 1995). A precipitate loss of 700 million fish was estimated for cod older than age 2 in 1991, corresponding to an average M value of 1.14 compared with the level of 0.2 assumed in cod-stock assessments (Shelton and Lilly 2000). However, the hypothesis of a sudden increase in M in 1991 was rejected (Hutchings and Myers 1994; Myers and Cadigan 1995), and fishing mortality was regarded as sufficient cause for the collapse of the stock (Myers et al. 1996; Walters and Maguire 1996). Our estimates of mortalities F, M^{p}, M^{i}, and M^{m} before 1993 support the finding in Myers and Cadigan (1995). In particular, when the data up to 1995 are used (leaving out the data from 1996 and 1997), the estimated M^{m} in the early 1990s declines slightly.

Could a precipitate drop in cod biomass similar to that of the cod stocks off southern Labrador and eastern Newfoundland (Shelton and Lilly 2000) also have happened to the 4VsW cod stock? We take advantage of the estimates of annual variations in mortality and recruitment to explore population dynamics through the entire observation history. To reveal biomass loss due to various mortalities, we partitioned the total biomass loss of mature cod into four parts: loss due to F, M^{p}, 0.2 (or M^{m} if it is less than 0.2), and the portion of M^{m} beyond 0.2. Although the cod fishery in 4VsW appears

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to have collapsed over 1991 and 1992, the decline in survival of mature cod has taken place since 1985 (Fig. 9). Since 1988, the quantity of fish that died has been greater than that which survived. In 1992, the percent of mature cod that died reached a peak. Replenishment from age 4 cod has been low since 1985, except for the increases in 1990 and 1991, corresponding to the relatively high R estimates in 1987 and 1988. However, the abundance of surviving age 4 cod dropped dramatically in 1992 despite the fact that M^{i} and M^{m} remained at historically low levels. Off southern Labrador and eastern Newfoundland, young cod aged 4 and 5 in 1990 and 1991 resulting from high recruits in 1986 and 1987 were similarly predominant in the catches made just before the fishery closure, which was attributed to the relative absence of older fish (Myers et al. 1996). With M^{m} remaining around the historical average level of 0.2, it can be concluded that a high F value and insufficient recruitment of age 4 cod to the mature cod stock have contributed to the continuous decline in mature cod biomass.

To envisage the biomass dynamics of immature cod, we also partitioned the total biomass loss into four parts: loss due to F, M^{p}, average of the M^{i} estimates (or M^{i} if it is below the average), and the portion of M^{i} beyond its average. Before the fishery collapse, there were two periods when loss of immature cod biomass exceeded 50%, one in the early 1970s and another in the early 1980s. The large loss of immature cod biomass in the early 1980s may have contributed to the reduction in recruitment of age 4 cod to the mature cod stock. The causes of the large biomass loss are unknown, but it is consistent with the widely discussed period of extensive discarding of undersized fish (Mohn et al. 1998). Overall, we conclude that fishing mortality may have been the primary cause of the collapse of the 4VsW cod stock.

It was suggested that the unbridled increase in F just before the collapse was caused by overestimation of stock size (Walters and Maguire 1996), statistical bias inherent in the estimation procedures (Myers et al. 1996), or increased concentration of cod at low stock size (Hutchings and Myers 1994; Hutchings 1996; Rose et al. 2000). Based on their statistical analysis, Myers et al. (1995) suggested that the cod stocks would recover after the moratorium on fishing. However, this has not happened up to this point, 10 years after the moratorium. Why are the stocks not recovering? What happened to the cod stocks after the collapse? Our M^{p}, M^{i}, and M^{m} estimates for the 4VsW cod stock after its collapse demonstrate that M^{p} became an important factor affecting the survival of immature cod in the 1990s. Throughout the 1990s, the proportion of immature cod that died was greater than that which survived. Mature cod may also have been subject to high natural mortality since the mid-1990s. Recruitment was low in the 1990s. These three factors have contributed to the failure of the stock to recover.

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Long-term effects of resource limitation on stream invertebrate drift

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Abstract: We examined the effects of resource limitation on stream invertebrate drift by reducing inputs of terrestrial detritus to a headwater stream in western North Carolina. In the treatment stream, leaf-litter was excluded for 6 years (September 1993 – August 1999), small woody debris was removed for 2 years (September 1996 – August 1998), and large and small woody debris was removed for 1 year (September 1998 – August 1999). Invertebrate abundance in the drift was significantly lower in the treatment stream during the study, but total biomass of invertebrate drift was similar. Although drift densities were higher in the reference stream, a greater proportion of total benthic invertebrate abundance and biomass drifted out of the treatment stream. The proportion of shredder, gatherer, and predator benthic abundance in the drift was significantly greater in the treatment stream, but scraper proportions were higher in the reference stream and filterer proportions were similar for the two streams. Combined data from both streams indicated that the relationship between drift densities and benthic abundance was positive and significant. Our results demonstrate that bottom-up effects of resource reduction in a detrital-based stream influence invertebrate drift, increasing the proportion of the benthic community emigrating from the detritus-poor stream.

Résumé : La réduction des apports de détritus terrestres dans un ruisseau d'amont de la Caroline du Nord occidentale nous a permis d'étudier les effets de la limitation des ressources sur la dérive des invertébrés. Nous avons exclu la litière de feuilles pendant 6 ans (septembre 1993 - août 1999) du ruisseau expérimental et retiré pendant 2 ans (septembre 1996 - août 1998) les petits débris ligneux et pendant 1 an (septembre 1998 - août 1999) les débris ligneux, grands et petits. La densité des invertébrés dans la dérive était significativement plus basse dans le ruisseau expérimental pendant l'étude, mais la biomasse totale de la dérive des invertébrés était semblable dans les deux ruisseaux. Bien que la densité de la dérive ait été supérieure dans le ruisseau témoin, une plus grande proportion de la densité et de la biomasse totale d'invertébrés benthiques a quitté le ruisseau expérimental par dérive. Les proportions en densité d'invertébrés déchiqueteurs, collecteurs et prédateurs dans la dérive étaient plus importantes dans le ruisseau expérimental, alors que la proportion de râcleurs étaient plus grande dans le ruisseau témoin et les proportions de filtreurs étaient les mêmes dans les deux ruisseaux. Les données combinées des deux ruisseaux indiquent que la relation entre la densité de la dérive et l'abondance du benthos est positive et significative. Nos résultats démontrent que les effets ascendants de la réduction des ressources dans un système d'eau courante dont la chaîne alimentaire est à base de détritus influencent la dérive des invertébrés en augmentant la proportion de la communauté benthique qui émigre du ruisseau pauvre en détritus.

[Traduit par la Rédaction]

Introduction

Resource limitation (and more specifically food limitation) is a very important factor in the structuring of freshwater communities. Evidence of food limitation has been found in both freshwater lakes (Gonzalez and Frost 1992) and streams (Richardson 1991; Rosemond et al. 1993). In streams, food resource abundance can affect invertebrate interactions and processes, including competition (Kohler 1992), growth (Hershey et al. 1988), and the taxonomic composition and carrying capacity of the benthos (Peterson et al. 1993; Wallace et al. 1999).

Evidence for a relationship between food resources and aquatic invertebrate drift in both algal- and detritus-based streams has been accumulating (Warren et al. 1964; Richardson 1991; Hinterleitner-Anderson et al. 1992). In general, experiments by these investigators have shown that addition of food resources (whether algal or detrital) tends to decrease emigration of the individuals or functional groups under examination. This outcome suggests that individuals remain in stream areas where food resources are abundant but emigrate as resources become limiting.

Heterotrophic pathways dominate processes in forested headwater streams. A low level of primary production in these streams places great importance on energy flows originating from terrestrial organic matter sources (Webster et al. 1995). The large pool of organic carbon from these terrestrial sources may also impart a degree of stability to the system

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(Wetzel 1995). The significance of allochthonous organic matter to secondary production in forested headwater streams has been well documented (e.g., Webster et al. 1995; Wallace et al. 1999), as has the importance of the invertebrate community to the processing of allochthonous detritus that enters these streams (Wallace et al. 1991; Wallace and Webster 1996). However, the effects of detritus reduction on drift of the invertebrate community are not fully understood.

Single- and multi-species laboratory (Kohler 1985) and field (Warren et al. 1964; Mundie et al. 1983; Richardson 1991) studies have been conducted to examine the relationship between food abundance, benthic densities, and drift. However, most of these studies have supplemented naturally occurring resource levels (i.e., nutrients, algae, and detritus) to test for potential food limitation. Long-term ecosystem-level manipulations examining the effects of a reduced food resource on the drift of an entire invertebrate community are lacking.

We experimentally tested the effects of an ecosystem-level exclusion of detritus entering a forested headwater stream to determine if drift of the invertebrate community is a function of food abundance. Our hypothesis was that if limiting food resources influence drift, then the proportion of benthic animals emigrating by drift should be greater if the amount of organic detritus is lower. Furthermore, we hypothesized that the effect should be greater for those functional groups most affected by litter exclusion, which included shredders, gatherers, and predators (Wallace et al. 1999).

Materials and methods

Study sites

This study was conducted in two headwater streams within the Coweeta Hydrologic Laboratory in western North Carolina. Coweeta is a 1625-ha drainage basin in the Blue Ridge Province of the southern Appalachian Mountains. A detailed description of the Coweeta basin is given in Swank and Crossley (1988). The reference and treatment streams are first order and have a southern aspect. The reference stream drains catchment 53, while the treatment stream drains catchment 55. The streams have similar temperature regimes and physical and chemical characteristics (Table 1). Vegetation in both catchments consists of hardwoods dominated by oak (*Quercus* spp.) and yellow poplar (*Liriodendron tulipifera*). A dense understory of rhododendron (*Rhododendron maximum*) provides shade throughout the year and maintains primary production at very low levels (Webster et al. 1983).

Leaf-litter was excluded from the treatment stream starting in August 1993 by a 1.2-cm-mesh gillnet canopy and a 20-cm-high lateral fence extending from the headwater spring seep downstream for 170 m. The sides of the stream remain open to allow colonization by aerial adult invertebrates. In addition to excluding leaf-litter, all small wood (≤10 cm in diameter) was removed from the length of the treatment section in August 1996. Large wood (>10 cm in diameter) was removed from the stream in August 1998. Buried wood that surfaced during storm flows and wood that entered the stream by other means was removed seasonally. The exclusion of litter and the removal of small and large wood resulted in (*i*) reductions in benthic invertebrate abundance, biomass, and production (Wallace et al. 1997, 1999), (*ii*) less export of dissolved organic carbon (Meyer et al. 1998), (*iii*) less export of fine and coarse particulate organic matter, and (*iv*) less fine and coarse benthic organic matter (J.B. Wallace, S.L. Eggert, J.R. Webster, and J.L. Meyer, University of Georgia, Athens, Ga., unpublished data) compared with the reference stream and with pretreatment conditions.

Table 1. Physical parameters of the reference and treatment streams at Coweeta Hydrologic Laboratory in western North Carolina.

Variable	Reference	Treatment
Catchment		
Area (ha)	5.2	7.5
Elevation (m above sea level)	829	810
Channel length (m)	135	170
Wetted width (m)[a]	0.7–1.2	1.2–1.6
Bankful channel area (m^2)	327	373
Bedrock outcrop (% composition)	27	13
Mixed substrates (% composition)	73	87
Discharge (for 1995–1999) ($L \cdot s^{-1}$)		
Average (5 year average)	0.95	1.53
Maximum (5 years)	32.13	71.45
Average discharge during drift sampling[b]	0.83	1.27
Temperature (for 1985–1997) (°C)		
Annual average (12-year average)	12.2	12.2
Annual degree-days (12-year average)	4485	4512
Maximum (12 years)	20.3	20.1
Minimum (12 years)	0.7	0.7

[a]Average wetted widths measured during dry and wet periods.
[b]Drift sampling average for discharge measurements on sampling dates only (April 1995 – August 1999).

Drift sampling

Drift samples were collected from both streams using standard drift nets (mesh size 234 µm). These samples were collected roughly twice a month during nonstorm periods from April 1995 to August 1999. The nets were positioned to sample the entire stream discharge, which was calculated from stage heights taken at a 30-cm H-flume located at the base of each catchment. Mean discharge for each sampling date was calculated from stage heights measured before net placement and immediately after net removal. Drift sampling began at dusk and was completed soon after sunrise. Analysis of day and night drift samples from the study streams (E.R. Siler and J.B. Wallace, unpublished data) as well as from another Coweeta stream (O'Hop and Wallace 1983) showed that a diel drift periodicity exists for some species but not for others. Therefore, in order to be conservative, we conducted our sampling only during the hours of darkness.

The contents of the drift nets were placed on ice and taken to the laboratory. Less than 24 h after being collected, organic matter in the samples (including invertebrates) was removed from any inorganic substrate by using water to suspend the organic matter and passing it through nested 1-mm and 250-µm sieves. Invertebrates were removed from organic matter fractions with the aid of Phloxine B dye and a dissecting microscope and preserved in 6–8% formalin. All invertebrates were removed from >1-mm samples; those retained on the 250-µm sieve were subsampled when necessary (1/8 to 1/64 of the whole sample) using a sample splitter (Waters 1969) as described by Lugthart and Wallace (1992).

Insects were identified to genus or species when possible, except for chironomids, which were identified as Tanypodinae or non-Tanypodinae (Merritt and Cummins 1996; Wiggins 1996). Noninsects were identified to the ordinal level or higher (Thorp and Covich 1991). Functional feeding groups were determined from designations given by Merritt and Cummins (1996). Invertebrates were measured to the nearest millimetre using a graduated stage micrometer, and biomass was calculated for all taxa using length–weight regressions (Benke et al. 1999). Drift densities were calculated for

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abundance (individuals per 100 m^3) and biomass (milligrams ash-free dry mass (AFDM) per 100 m^3) following Smock (1996).

Mean monthly benthic invertebrate abundance (individuals per square metre) and biomass (milligrams AFDM per square metre) were calculated from four benthic core and three rock face samples taken monthly in each stream throughout the study period (Wallace et al. 1999). Mean monthly benthic core and rock face invertebrate densities (individuals per square metre) and biomass (milligrams AFDM per square metre) were habitat weighted for percentage of mixed substrate and rock face habitats in each stream (Table 1) to obtain total monthly habitat-weighted invertebrate densities and biomass for each stream. To determine the proportion of total benthic invertebrate abundance and biomass in the drift of each stream during a 24-h period, mean monthly drift rates were calculated as total abundance (individuals per 24 h) and total biomass (mg AFDM per 24 h) in the drift and divided by monthly habitat-weighted benthic abundance or biomass.

Statistical analysis

The complexity of whole-ecosystem manipulations makes them inherently more realistic than small-scale replicated studies (Schindler 1998), and the need for ecosystem-level experiments has been extolled (Carpenter et al. 1995; Carpenter 1996). Because of the costs and difficulties associated with replicating an ecosystem-level experiment, we acknowledge the presence of psuedoreplication (Hurlbert 1984). Additionally, a lack of pretreatment data prevented us from using nonparametric statistics often associated with analysis of whole-ecosystem manipulations (Carpenter et al. 1989). However, we believe that the length of the study, the scale of the experiment, and the strength of the results support our conclusions.

Monthly means for abundance and biomass were calculated from the raw data for community, functional feeding groups, and drift densities of selected taxa. Yearly means (September–August) were calculated from monthly means for all years, although year 1 (1995) only included data from April 1995 to August 1995. Seasonal means were calculated for spring (April, May, June), summer (July, August, September), autumn (October, November, December), and winter (January, February, March). All data were $\log_{10}$ or arcsine square root transformed to correct for heteroscedasticity and nonnormality. Some, but not all, transformations were successful in correcting for these two factors. A three-way analysis of variance (ANOVA) (SPSS release 10.0.1) was then used to test for effects of treatment, year, and season. Significant ANOVAs were followed by Tukey's multiple comparisons. Linear regression analysis was used to describe the relationship between invertebrate drift densities and benthic invertebrate abundance and the relationship between the proportion of the benthos in the drift and benthic abundance.

Results

Composition of the drift

Gatherers comprised the greatest proportion of drift density in both streams. In the reference stream, the sequence of relative abundance of functional feeding groups was gatherers > predators > filterers > shredders > scrapers. This sequence was similar to that found for the treatment stream, except that shredders were third most common in the drift, followed by filterers and scrapers.

Scrapers comprised a very small percentage (usually <2.0%) of drift abundance in both streams. *Baetis* sp. and *Epeorus* sp. were the most common scrapers, but neither taxon comprised more than 1.1% of the total drift in any year. Scrapers comprised a larger portion of mean yearly drift biomass, constituting 1.1–12.7 and 5.0–9.7% of total drift biomass in the reference and treatment streams, respectively.

Shredders comprised 3.1–15.5% of annual abundance and 21.0–31.8% of drift biomass and were most common during autumn in both streams. The proportion of shredders drifting from the treatment stream increased each autumn as litter exclusion and wood removal continued. Shredders in the treatment stream increased from 14.8% of total drift in autumn 1995 to 41.1% in autumn 1999, surpassing gatherers as the most common functional feeding group in the drift. This was a result of large increases in the drift of Peltoperlidae, the most common shredder in the drift (Table 2).

Gatherers were most common in winter and spring and comprised the greatest percentage of the drift in all seasons in the reference (45.4–88.3%) and treatment (36.2–77.7%) streams, except in autumn 1998. Copepods were the most common gatherer in the reference stream, representing 33.0–46.2% of mean yearly drift. In the treatment stream, non-Tanypodinae chironomids were the most common gatherer (Table 2), comprising 26.8–40.7% of mean yearly drift. Unlike drift abundance, gatherers did not always dominate drift biomass. Copepods and chironomids were the most abundant taxa in the drift, but they accounted for only a small proportion (2.5–9.0%) of drifting biomass (Table 2).

In the reference stream, filterers comprised 8.3–15.2% of annual abundance and 10.0–23.3% of biomass. Filterers in the treatment stream comprised 4.4–10.7 and 8.7–16.1% of drift abundance and biomass, respectively. *Dixa* sp. was the most common filterer in the drift, whereas the hydropsychids *Diplectrona modesta* and *Parapsyche cardis* comprised the largest proportion of biomass (Table 2).

Predators comprised 11.3–25.6% of annual abundance in both streams. Aquatic mites (Acari) dominated predator abundance in both the reference and treatment streams (Table 2). Acari comprised only 1.2–3.5% of total biomass in the drift of both streams, while predators as a group comprised 15.0–35.8%. *Lanthus* sp., *Beloneuria* sp., and *Isoperla* sp. contributed the most to predator biomass in the drift for both streams (Table 2).

Invertebrate drift abundance and biomass

Mean monthly drift densities (individuals per 100 m^3) were significantly lower in the treatment stream than in the reference stream (Fig. 1*a*; Table 3). Mean drift density in the reference stream over the course of the study was 2904 (SD, ±394) individuals·100 m^{-3}, while the mean for the treatment stream was only 888 (SD, ±94) individuals·100 m^{-3}. Mean drift densities in the reference stream were higher than in the treatment stream in 47 of the 53 months sampled. A significant difference among years was found but no clear temporal pattern was evident (Fig. 1*a*). A clear pattern of decreasing drift densities during years 3–5 would have indicated additional effects of small and large wood removal on drift. Seasonal drift densities differed as well, with drift in winter being lower than in any other season (Table 3). Although the year × season interaction was significant (Table 3), no clear pattern was evident. Individual functional feeding group drift densities also differed between streams. Shredders, gatherers, filterers, and predators were all significantly lower in the treatment stream (Table 4; Fig. 2). Scraper drift densities were not significantly different between streams.

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Table 2. Mean annual drift densities (individuals·100 m^{-3}) and drift biomass (mg AFDM, in parentheses) for invertebrate functional feeding groups and dominant taxa in the reference and treatment streams.

	Year 1 (1995)[a]		Year 2 (1995–1996)		Year 3 (1996–1997)		Year 4 (1997–1998)		Year 5 (1998–1999)	
Functional feeding group	Reference (n = 14)	Treatment (n = 14)	Reference (n = 23)	Treatment (n = 23)	Reference (n = 21)	Treatment (n = 21)	Reference (n = 26)	Treatment (n = 26)	Reference (n = 23)	Treatment (n = 23)
Total scrapers	13.6 (6.6)	8.6 (1.6)	24.1 (3.4)	4.3 (1.3)	16.3 (3.7)	7.4 (3.5)	19.0 (0.4)	8.9 (1.9)	4.4 (0.6)	12.2 (2.0)
Baetis sp.	10.6 (0.3)	2.7 (0.2)	18.7 (0.8)	0.3 (0.1)	11.3 (0.5)	3.0 (0.3)	7.5 (0.1)	1.5 (0.3)	1.8 (0.3)	5.1 (1.4)
Epeorus sp.	2.0 (5.8)	3.5 (1.4)	4.0 (1.8)	2.0 (1.1)	3.3 (3.1)	3.5 (3.1)	5.2 (0.1)	4.3 (1.6)	0.3 (0.0)	3.6 (0.5)
Total shredders	109.5 (21.9)	28.6 (6.7)	97.6 (16.9)	65.2 (9.8)	50.5 (8.4)	58.8 (6.4)	161.4 (9.5)	60.6 (4.8)	169.7 (24.1)	285.2 (10.4)
Peltoperlidae	77.6 (19.8)	8.9 (3.9)	55.3 (11.9)	46.1 (6.5)	30.0 (5.8)	33.3 (3.6)	71.6 (7.1)	36.4 (4.2)	116.8 (13.7)	265.0 (9.3)
Leuctra spp.	10.6 (0.6)	7.7 (0.5)	24.0 (1.1)	7.0 (0.6)	9.9 (0.3)	9.8 (0.2)	28.4 (0.4)	12.5 (0.1)	31.0 (3.2)	12.0 (0.3)
Total gatherers	1349.8 (4.3)	690.5 (12.4)	2181.0 (7.3)	617.7 (8.9)	991.2 (3.7)	494.3 (5.1)	3122.1 (10.3)	537.6 (4.2)	1899.7 (14.1)	418.6 (10.2)
Chironomidae	391.9 (0.7)	277.1 (0.6)	502.8 (1.3)	248.2 (0.7)	265.1 (1.1)	233.0 (0.6)	965.9 (2.4)	302.5 (0.5)	781.6 (2.4)	278.2 (0.9)
Copepoda	611.9 (0.6)	226.0 (0.2)	1243.9 (1.2)	203.6 (0.2)	508.9 (0.5)	144.3 (0.1)	1567.8 (1.6)	133.1 (0.1)	799.7 (0.8)	55.9 (0.1)
Stenonema sp.	3.0 (0.4)	6.0 (6.7)	49.7 (2.0)	8.7 (5.2)	31.7 (1.2)	12.4 (2.3)	17.3 (3.7)	2.9 (2.6)	19.3 (9.5)	14.6 (8.2)
Paraleptophlebia sp.	71.3 (1.3)	29.4 (3.2)	3.6 (0.03)	9.6 (0.6)	5.3 (0.05)	5.9 (0.4)	2.0 (0.1)	8.1 (0.2)	2.0 (0.0)	4.3 (0.2)
Total filterers	431.0 (4.4)	65.5 (2.3)	304.8 (4.4)	61.4 (2.7)	231.5 (3.1)	39.6 (1.1)	478.8 (12.4)	50.5 (1.6)	253.4 (4.6)	65.8 (1.9)
Dixa sp.	70.2 (0.4)	30.1 (0.2)	201.5 (1.6)	36.5 (0.3)	137.5 (0.7)	28.6 (0.1)	195.3 (1.3)	24.3 (0.1)	146.1 (1.0)	21.6 (0.3)
Diplectrona modesta	327.1 (2.8)	24.7 (0.3)	64.7 (0.7)	16.0 (1.6)	25.6 (0.9)	5.1 (0.3)	114.4 (6.4)	4.5 (0.5)	60.9 (1.0)	23.1 (0.5)
Parapsyche cardis	7.0 (0.9)	3.2 (0.9)	2.1 (1.2)	0.1 (0.1)	14.1 (1.0)	1.8 (0.6)	84.1 (3.7)	14.7 (0.1)	21.7 (1.9)	5.4 (0.3)
Total predators	296.5 (15.9)	175.7 (12.8)	407.1 (9.4)	261.1 (5.0)	282.6 (5.4)	186.7 (10.3)	807.5 (52.8)	158.0 (8.8)	405.9 (8.2)	125.5 (2.7)
Acari	156.5 (0.4)	114.9 (0.3)	217.7 (0.6)	147.0 (0.4)	188.3 (0.5)	115.6 (0.3)	634.6 (1.7)	124.6 (0.3)	235.6 (0.6)	84.6 (0.2)
Isoperla spp.	15.3 (0.3)	9.2 (0.3)	18.7(0.7)	5.4 (0.3)	9.6 (0.3)	115.6 (0.1)	10.4 (0.2)	124.6 (0.2)	19.1 (0.3)	84.6 (1.0)
Beloneuria sp.	20.5 (14.6)	1.9 (5.8)	3.7 (3.0)	2.3 (2.3)	2.6 (0.6)	0.3 (2.4)	2.7 (3.9)	0.3 (3.1)	0.0 (0.0)	0.0 (0.0)

Note: One year consisted of data from September to August. Drift data for years 1–5 include 2 years of litter exclusion (years 1 and 2), 2 years of litter exclusion and removal of small woody debris (years 3 and 4), and 1 year of litter exclusion plus removal of small and large woody debris (year 5).

[a]Year 1 only includes samples from April 1995 to August 1995.

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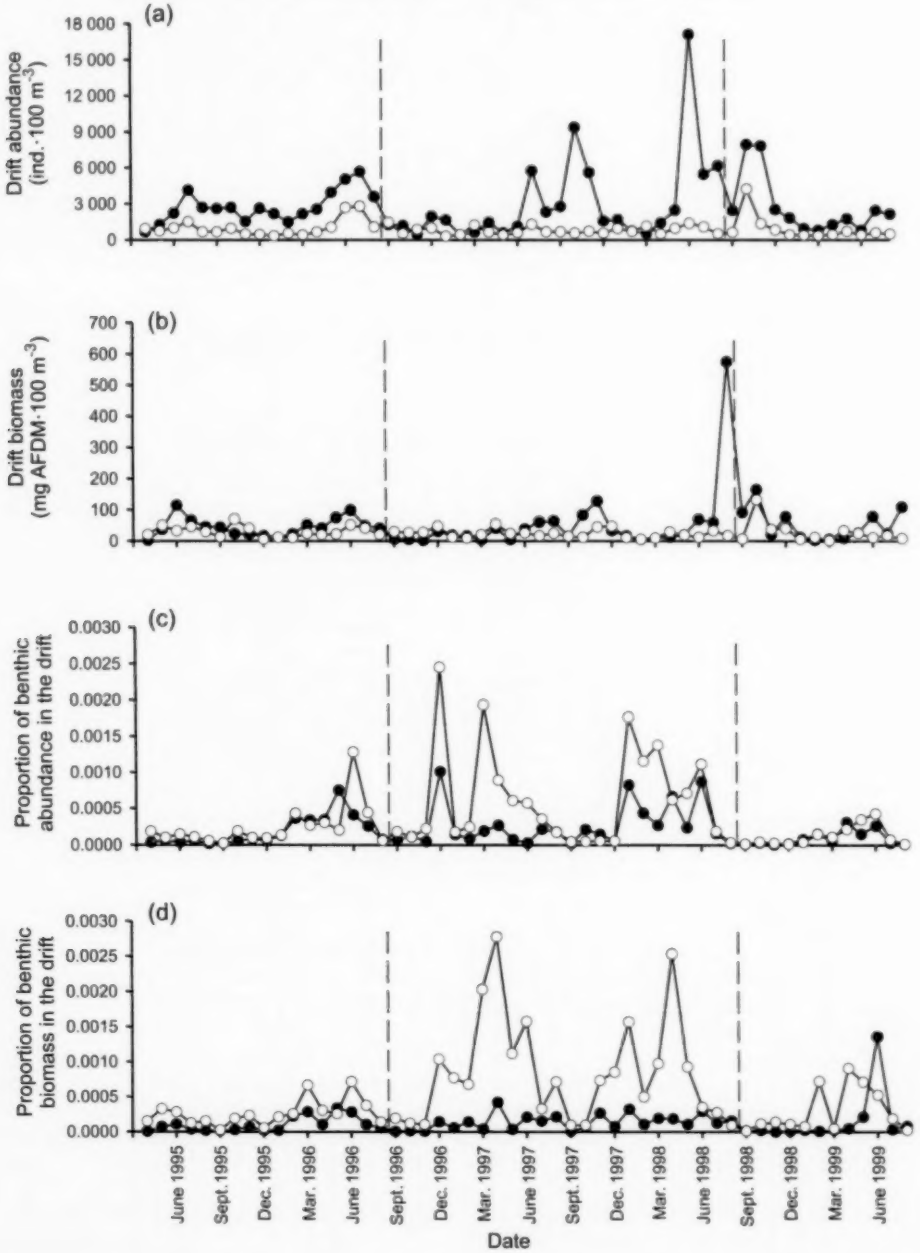
Fig. 1. Mean monthly drift densities for (*a*) abundance, (*b*) biomass, (*c*) proportion of benthic abundance, and (*d*) proportion of benthic biomass in the drift of the reference stream (solid circles) and treatment stream (open circles). The vertical dashed line on the left indicates when small wood was removed, and the one on the right indicates when large wood was removed. For all figures drift data for years 1–5 include 2 years of litter exclusion alone (years 1 and 2), 2 years of litter exclusion plus removal of small woody debris (years 3 and 4), and 1 year of litter exclusion plus removal of small and large woody debris (year 5).



Unlike abundance, mean monthly drift biomass (milligrams AFDM per 100 m^3) was not significantly different between streams (Fig. 1*b*; Table 3). Mean drift biomass in the reference stream for the whole study period was 50.97 (SD, ±11.25) mg AFDM·100 m^{-3}, while the mean in the treatment stream was 26.64 (SD, ±2.91) mg AFDM·100 m^{-3}. Although not significantly different, mean drift biomass was higher in the reference stream in 38 of the 53 months sampled. Biomass was not significantly different among years but it was different among seasons (Table 3), being lower in winter than in any other season. Scraper, gatherer, and predator biomass in the drift was similar between streams, whereas greater shredder

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Table 3. Results from three-way ANOVAs of drift density and biomass for reference versus treatment streams for the duration of the study (April 1995 – August 1999).

Source of variation	df	MS	*F*
Drift density (individuals·100 m^{-3})			
Treatment (reference vs. treatment)	1	4.76	87.53***
Year	4	0.18	3.39*
Season	3	0.54	9.93***
Treatment × year	4	0.08	1.54
Treatment × season	3	0.10	1.78
Year × season	10	0.17	3.1**
Treatment × season × year	10	0.09	1.75
Residual	70	0.05	
Drift biomass (mg AFDM·100 m^{-3})			
Treatment (reference vs. treatment)	1	0.25	1.83
Year	4	0.10	0.73
Season	3	1.36	9.96***
Treatment × year	4	0.27	2.00
Treatment × season	3	0.35	2.57
Year × season	10	0.28	2.07*
Treatment × season × year	10	0.12	0.91
Residual	70	0.14	

Note: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

and filterer biomass drifted out of the reference stream (Table 4; Fig. 3).

Proportion of benthic abundance and biomass in the drift

Despite significantly lower invertebrate drift densities in the treatment stream, the proportion of benthic invertebrate abundance in the drift of the treatment stream was significantly higher than in the reference stream (Fig. 1*c*; Table 5). The mean proportion of benthic abundance in the drift over the study period was 0.0198% (SD, ±0.0032%) for the reference stream, while mean for the treatment stream was 0.0389% (SD, ±0.0073%). The mean proportion of benthic abundance in the drift of the treatment stream was higher than in the reference stream in 35 of the 53 months sampled. A significant difference among years was found (Table 5), with the proportion of benthic abundance in the drift in year 5 being significantly lower than in any other year. Significant seasonal differences were also found (Table 5), as the proportion of drift in winter and spring was significantly greater than in summer and autumn. Again, although the year × season interaction was significant (Table 5), no clear pattern existed.

After adjusting for benthic abundance, between-stream comparisons were also made for the proportion of each functional feeding group in the drift. The proportion of shredders, gatherers, and predators in the drift was significantly greater in the treatment stream (Table 4; Fig. 4). The proportion of scrapers was significantly greater in the reference stream, whereas the proportion of filterers was not significantly different between streams (Table 4; Fig. 4).

A greater proportion of benthic invertebrate biomass drifted out of the treatment stream relative to the reference stream. After adjusting for habitat-weighted benthic biomass, the proportion of benthic biomass in the drift of the treatment stream was significantly greater than in the reference stream (Table 5; Fig. 1*d*). For the whole study period, the mean proportion of benthic biomass in the drift of the reference stream was 0.0131% (SD, ±0.0028%), while the treatment stream mean was 0.0537% (SD, ±0.0084%). The mean proportion of benthic biomass in the drift of the treatment stream was higher than for the reference stream in 48 of the 53 months sampled. The proportion of shredder, gatherer, and predator biomass in the drift was significantly greater in the treatment stream (Table 4; Fig. 5). However, the proportion of scraper and filterer biomass was not different between streams (Table 4; Fig. 5). For the proportion of total benthic abundance in the drift, there was a significant difference among years, but no apparent temporal pattern was found (Table 5). The proportion of total biomass also differed significantly among seasons (Table 5), being higher in winter and spring than in summer and autumn.

Relationships between drift and benthic abundance

When data from both streams were combined, drift densities were significantly related to benthic abundance (Fig. 6*a*). However, when data from each stream were analyzed separately, neither the reference nor the treatment stream displayed significant relationships between drift density and benthic abundance. An inverse relationship was found for both streams when we examined the relationship between the proportion of benthic abundance in the drift and benthic densities (Fig. 6*b*). The slopes of the regression lines were significantly different between streams (*t* test, $P < 0.001$).

Size comparisons of individuals in the drift and benthos

We compared the mean size (milligrams AFDM) of individuals in the drift with that of those in the benthos from each catchment for some common taxa to determine if individuals in the drift were smaller than those in the benthos during the study period. In the reference stream, the most common taxa in the drift (with the exception of *Baetis*) either showed no size difference between the benthos and drift or were significantly smaller in the drift than in the benthos (Table 6). In contrast with the reference stream, several taxa in the treatment stream (with the exception of the filterers *P. cardis* and *D. modesta*) were larger in the drift than in the benthos (Table 6).

Discussion

Previously, studies examining the effects of food resources on invertebrate communities, for either benthic densities or drift, have used naturally occurring levels of resources and made subsequent increases in the resource to examine potential food limitation (e.g., Hildebrand 1974; Richardson 1991; Hinterleitner-Anderson et al. 1992). Wallace et al. (1997, 1999) demonstrated the ecosystem-level importance of terrestrial detrital inputs to secondary production by excluding terrestrial detritus and removing wood from the stream. Leaf-litter exclusion and wood removal resulted in decreased abundance, biomass, and secondary production of the benthic invertebrate community when compared with pretreatment data and the reference stream.

In the present study, we examined drift of the invertebrate communities in these same study streams. Drift densities of functional feeding groups that rely directly (shredders, gath-

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Table 4. Results from three-way ANOVAs of drift density, drift biomass, proportion of benthic abundance in the drift, and proportion of benthic biomass in the drift for reference versus treatment streams for the duration of the study (April 1995 – August 1999).

Functional feeding group	Drift density (individuals·100 m^{-3})		Drift biomass (mg AFDM·100 m^{-3})		Proportion of benthic abundance		Proportion of benthic biomass	
	Reference	Treatment	Reference	Treatment	Reference	Treatment	Reference	Treatment
Scrapers	ns		ns		***		ns	
Shredders	*		**			***		***
Gatherers	***		ns			**		***
Filterers	***		***		ns		ns	
Predators	**		ns			***		**

Note: Asterisks indicate which stream is significantly greater: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; ns, no significant difference between streams.

Table 5. Results from three-way ANOVAs of the proportion of benthic abundance and biomass in the drift of the reference and treatment streams.

Source of variation	df	MS	F
Proportion of benthic abundance			
Treatment (reference vs. treatment)	1	0.05	10.07**
Year	4	0.04	9.17***
Season	3	0.07	15.17***
Treatment × year	4	0.007	1.49
Treatment × season	3	0.004	0.95
Year × season	10	0.02	3.68**
Treatment × season × year	10	3.72	0.82
Residual	70	0.004	
Proportion of benthic biomass			
Treatment (reference vs. treatment)	1	0.003	53.30***
Year	4	0.0004	6.90***
Season	3	0.0008	15.00***
Treatment × year	4	0.0001	2.78*
Treatment × season	3	0.0001	2.55
Year × season	10	0.00007	1.40
Treatment × season × year	10	0.00004	0.80
Residual	70	0.00005	

Note: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

erers, and filterers) or indirectly (e.g., predators) on detritus were significantly greater in the reference stream. This result was expected, as gatherer, shredder, and predator abundance in the benthos of the treatment stream has declined significantly since the start of litter exclusion (Wallace et al. 1999). In contrast, scraper drift densities did not differ between streams. This result agrees with the lack of response in benthic densities of scrapers in the treatment stream (Wallace et al. 1999). Thus, absolute densities of invertebrates in the drift and in the benthos have shown similar responses to litter exclusion.

Results for absolute drift density are in marked contrast with that for the proportion of the benthic community in the drift. Larger proportions of benthic invertebrates were drifting in the treatment stream than in the reference stream. Previous authors have shown that when food resources are low, the proportion of the benthos in the drift is usually higher than when resources are abundant (Warren et al. 1964; Hildebrand 1974; Hinterleitner-Anderson et al. 1992). We found that the proportion of benthic shredders, gatherers, and predators in the drift of the treatment stream was significantly greater than in the reference stream. This suggests a lower carrying capacity in the treatment stream, brought on by reduction of the resource base. While normal levels of colonization were likely possible because of downstream areas and nearby "source" streams, resources were limited for early instars. Our results suggest that this induced a larger proportion of benthic emigration in the food-limited treatment stream.

Waters (1966) hypothesized that drift is a function of the degree to which the carrying capacity of a stream tends to be exceeded. According to this hypothesis, all functional feeding groups were at least somewhat resource limited in our study streams. However, detritivores (i.e., shredders and gatherers) and predators, which rely heavily on detritivores as prey, were more resource limited in the treatment stream as evidenced by a greater proportion of them in the drift compared with the reference stream. In previous studies of detritus-based systems, increases in organic matter concentrations have resulted in increased benthic densities of detritivores (particularly shredders) but decreased drift (Warren et al. 1964; Mundie et al. 1983; Richardson 1991). In our study, which severely decreased organic matter inputs, the proportion of shredders in the drift of the treatment stream increased during autumn each year. In fact, in autumn 1998, drift of shredders surpassed that of gatherers. Although benthic densities of shredders were significantly lower in the treatment stream, their drift densities were approximately two times greater than in the reference stream in autumn 1996 and autumn 1998 directly after small (August 1996) and large wood removal (August 1998). We suggest this is a consequence of decreasing food supply for shredders. With ongoing litter exclusion, benthic organic matter declined, and shredders (mainly Peltoperlidae and *Leuctra* spp.) encountered an extremely resource-limited environment and drifted in greater proportions, presumably in search of more abundant food resources. Also, the large peak in fall shredder drift proportions in the treatment stream is evidence for continued colonization of the benthos by aerial adults.

No between-stream differences in the proportion of filterer benthic abundance or biomass in the drift were found, suggesting that drift of filterers may not be affected by litter exclusion. Wallace et al. (1999) noted that the direct coupling between terrestrial coarse particulate organic matter and filterers is not as tight as for other detritivores (i.e., gatherers and shredders). Filter feeders use the current to exploit food resources created in upstream habitats, expending very little energy on food acquisition (Wallace and Webster 1996). This feeding mechanism allows filterers to (*i*) reach a very high

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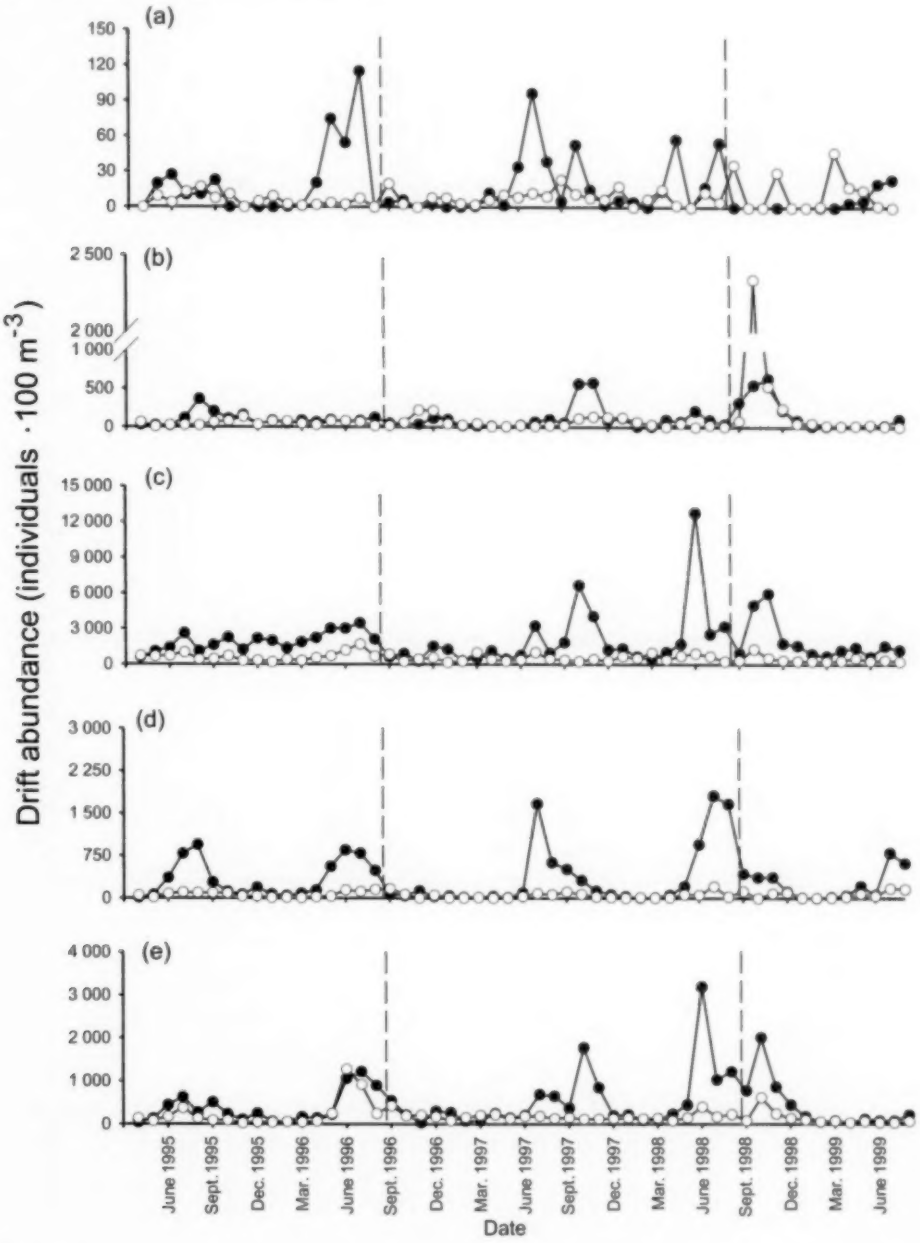
Fig. 2. Mean monthly drift densities for (*a*) scrapers, (*b*) shredders, (*c*) gatherers, (*d*) filterers, and (*e*) predators in the reference stream (solid circles) and treatment stream (open circles). The vertical dashed line on the left indicates when small wood was removed, and the one on the right indicates when large wood was removed.



biomass per unit area (Wallace and Webster 1996) and (*ii*) not incur food limitation until resources are at extremely low levels. These levels have likely not yet been reached in the treatment stream. For example, fine particulate organic matter export (seston) from the treatment stream declined to 73% of reference levels by year 4 of litter exclusion (Wallace et al. 1999), and a smaller but continued decline is expected. However, inputs of organic matter from soil, throughfall, and bank runoff continue to enter the stream and contribute to seston concentrations (J.B. Wallace, E.R. Siler, and S.L. Eggert, University of Georgia, Athens, Ga., unpublished data). By year 6 of litter exclusion (which includes 3 years of small wood removal plus 1 year of large wood removal), about 425 g AFDM·m^{-2} stored organic matter still remained

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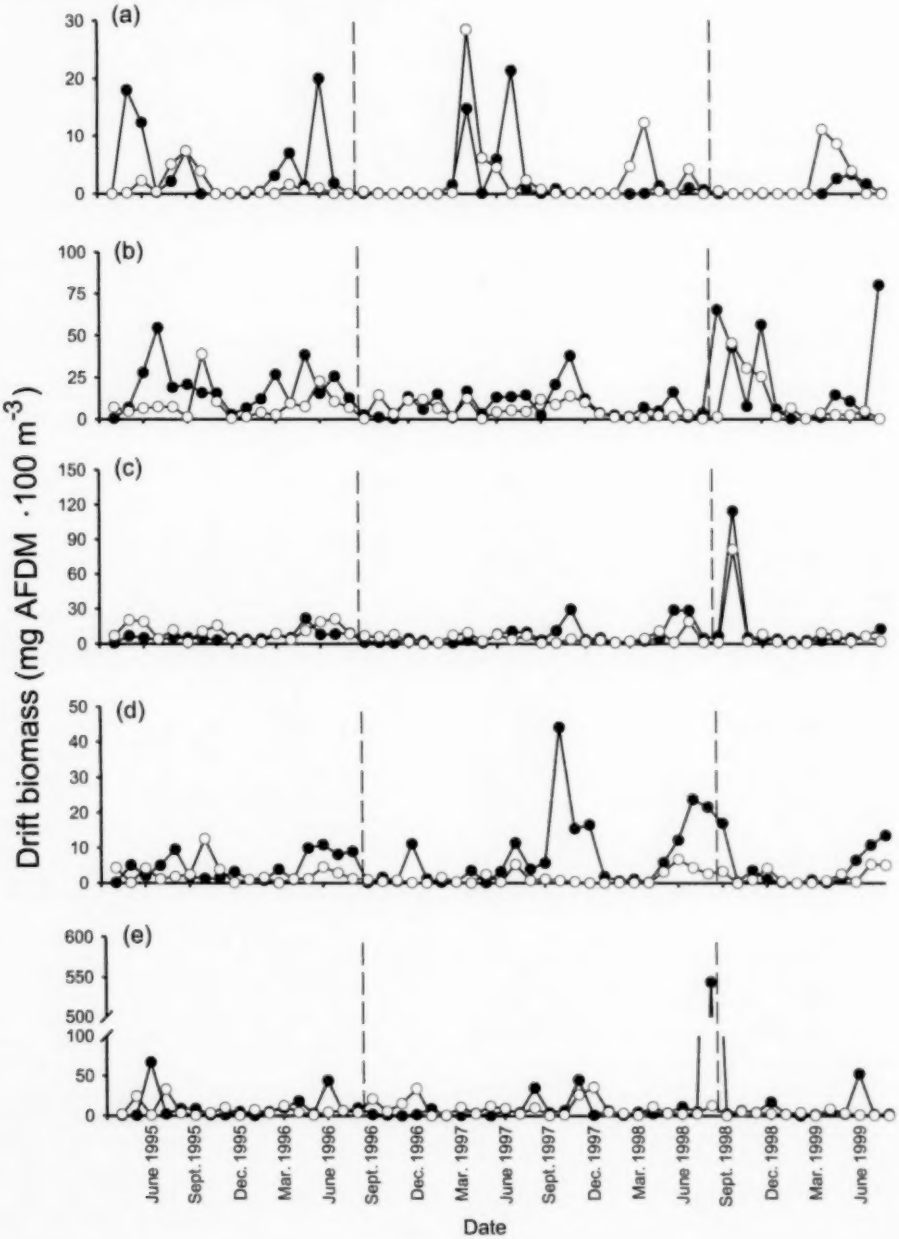
Fig. 3. Mean monthly drift biomass for (*a*) scrapers, (*b*) shredders, (*c*) gatherers, (*d*) filterers, and (*e*) predators in the reference stream (solid circles) and treatment stream (open circles). The vertical dashed line on the left indicates when small wood was removed, and the one on the right indicates when large wood was removed.



in the mixed substrates of the treatment stream (J.B.Wallace, S.L. Eggert, J.L. Meyer, and J.R. Webster, University of Georgia, Athens, Ga., unpublished data). Therefore, a source of seston still remains and is able to support filterer production in the treatment stream.

Scraper production has been unaffected by litter exclusion (Wallace et al. 1999). Unlike detritivores and predators, the proportion of scraper benthic abundance in the drift was significantly greater in the reference stream. Scrapers have been found to be food limited in some streams (Rosemond et al. 1993; Harvey et al. 1998) and are likely food limited in the heavily shaded headwater reaches of our study streams, as evidenced by their low abundance, biomass, and production (Wallace et al. 1999). Light is limiting in headwater streams at Coweeta (Lowe et al. 1986), and the absence of benthic organic matter in the treatment stream during late

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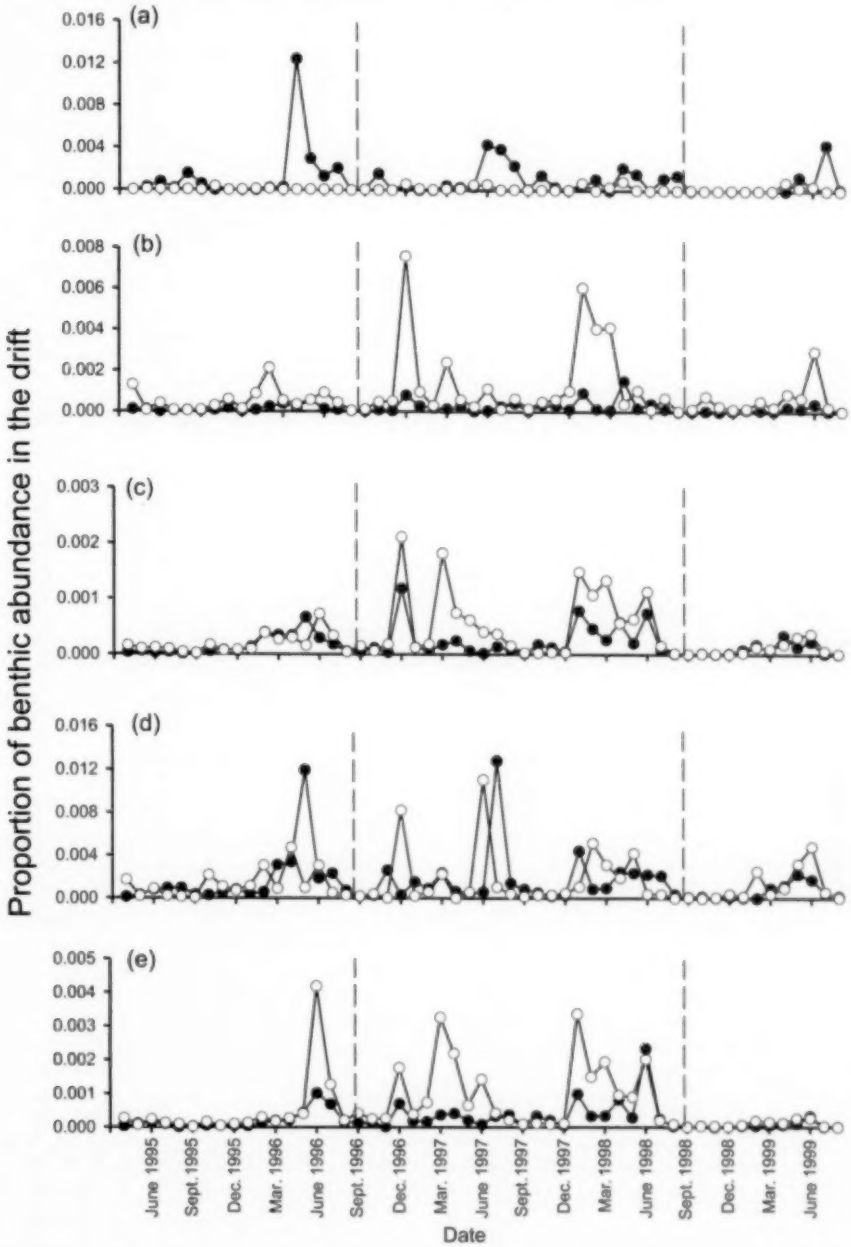
Fig. 4. Mean monthly proportion of benthic abundance in the drift for (*a*) scrapers, (*b*) shredders, (*c*) gatherers, (*d*) filterers, and (*e*) predators in the reference stream (solid circles) and treatment stream (open circles). The vertical dashed line on the left indicates when small wood was removed, and the one on the right indicates when large wood was removed.



autumn, winter, and early spring allowed more light to reach benthic substrates when the overstory canopy was absent. Visual observations during this time period also suggest higher algal standing crops in the treatment stream (E.R. Siler, personal observation). Significantly lower proportions of scrapers in the drift of the treatment stream may be a result of increased food resources. Other studies found that the proportion of scraper invertebrate abundance in the drift is smaller when food resources are greater (Warren et al. 1964; Hinterleitner-Anderson et al. 1992), and individual scrapers are less likely to enter the drift when high-quality food patches are available (Kohler 1985).

Relationships between drift and benthic abundance

Combined data from both streams revealed a positive relationship between benthic abundance and drift density. Links

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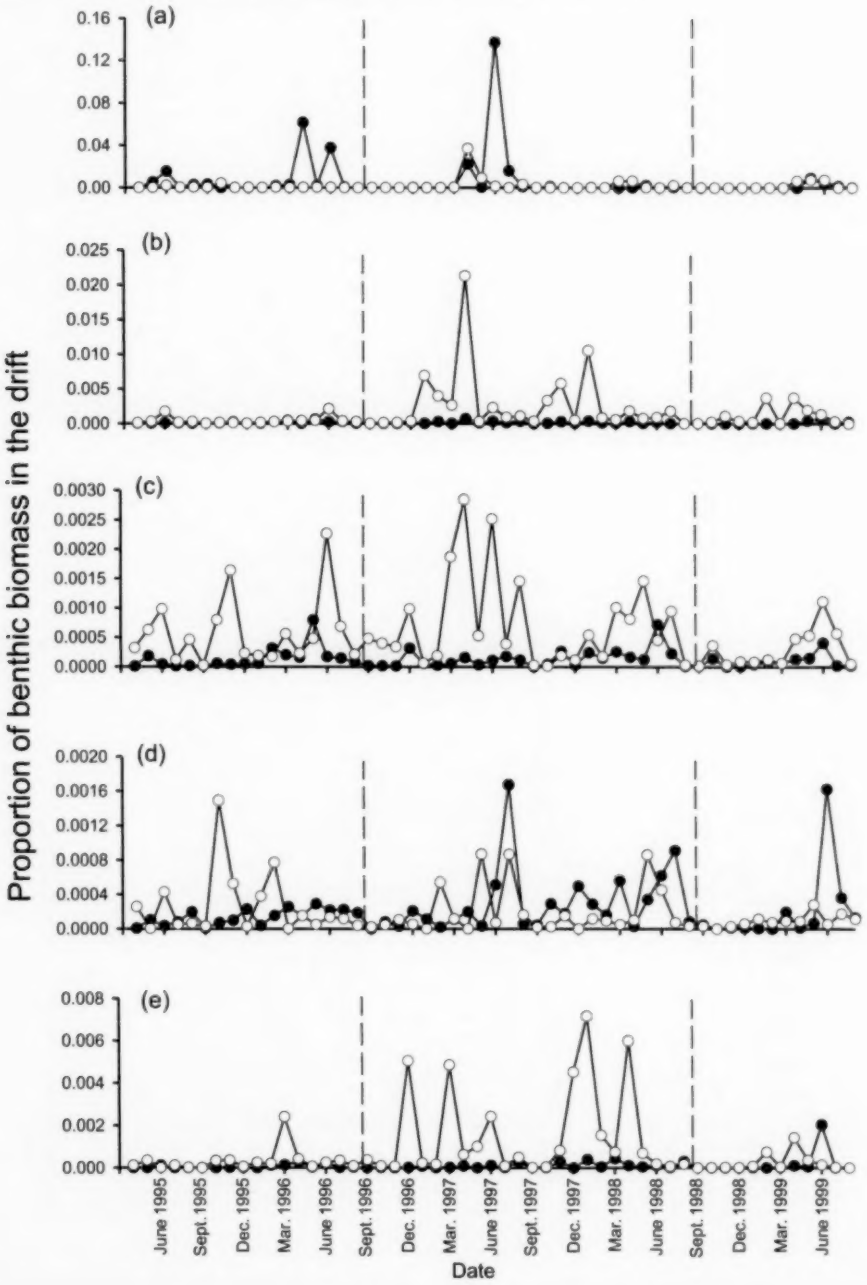
Fig. 5. Mean monthly proportion of benthic biomass in the drift for (*a*) scrapers, (*b*) shredders, (*c*) gatherers, (*d*) filterers, and (*e*) predators in the reference stream (solid circles) and treatment stream (open circles). The vertical dashed line on the left indicates when small wood was removed, and the one on the right indicates when large wood was removed.



between secondary production and drift in other regions suggest that mean drift rate might be used as an index of a stream's productive capacity (Waters 1961). Our results support Waters' (1961) suggestion, as decreased drift densities in the treatment stream corresponded to decreased secondary production. The extreme disparity between abundance, biomass, and secondary production between reference and treatment streams enhanced our ability to detect this trend. Annual fluctuations in benthic invertebrate abundance and drift from only one stream were not great enough to detect a significant relationship between benthic density and drift.

Inverse relationships existed when we examined the relation-

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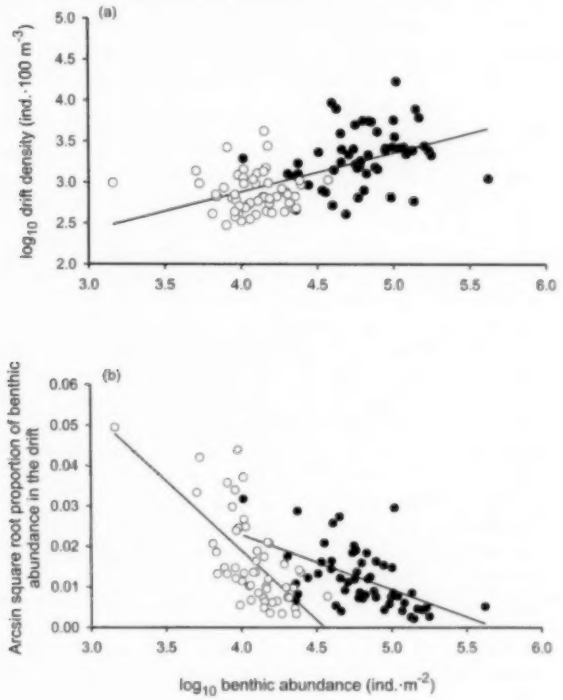
Fig. 6. Benthic abundance relationships with (*a*) drift density ($r^2 = 0.32$, $P < 0.001$) and (*b*) proportion of benthic abundance in the drift ($r^2 = 0.29$, $P < 0.001$ for the reference stream and $r^2 = 0.46$, $P < 0.001$ for the treatment stream). Mean monthly data from April 1995 to August 1999 for the reference stream (solid circles) and treatment stream (open circles).



ship between benthic abundance and the proportion of the benthos in the drift. We propose that this was a consequence of continued colonization of the benthos by aerial adults. Baer et al. (2001) found that colonization was continuing in the treatment stream, although at a significantly lower rate. Evidence of continued colonization along with elevated drift in proportion to the benthos suggests reduced carrying capacity in the treatment stream. Based on benthic samples, few invertebrates in the treatment stream reach terminal instars, while size comparisons of individuals in the drift show that more of these later instars are drifting. These results, combined with the elevated drift proportion, suggest that recruitment by aerial adults was primarily responsible for continued colonization of the treatment stream. However, our study was not designed to detect whether these adults were from downstream sources or other nearby streams, and therefore, we cannot make inferences about upstream flight and possible colonization cycle dynamics.

Effects of small and large wood removal on drift

Small and large wood removal had minimal effects on drift of the invertebrate community in the treatment stream, but some effects on shredders were evident. Total drift densities in years 3–5 (3 years of small wood removal plus an additional year of large wood removal) did not show any striking differences when compared with years 1 and 2. There was a significant effect of year on drift densities, but no treatment × year interaction for abundance or biomass, which suggests no additional effect of wood removal on drift of the invertebrate community in the treatment stream. Year 5 drift densities were somewhat lower than those of previous years in the treatment stream and did not show a peak in drift densities during the spring. The much lower discharge during year 5 likely resulted in the lower drift densities seen in both the treatment and reference streams. Average discharge in the treatment stream during drift sampling in year 5 was 0.60 $L \cdot s^{-1}$, while discharge in years 1–4 was 0.63 (April 1995 – August 1995), 1.27, 1.84, and 1.64 $L \cdot s^{-1}$, respectively.

Table 6. Mean size comparisons (mg AFDM·individual^{-1}, Mann–Whitney rank sum test) of common taxa from each functional feeding group between the drift and the benthos of the reference and treatment streams for the duration of the study (April 1995 – August 1999).

Functional feeding group	Reference		Treatment	
	Benthos	Drift	Benthos	Drift
Scrapers				
Baetis sp.	0.035	0.062*	0.036	0.189***
Epeorus sp.	1.203	3.005	0.869	2.605
Shredders				
Peltoperlidae	0.338	0.492	0.110	0.245*
Leuctra spp.	0.039	0.052	0.028	0.051
Gatherers				
Chironomidae	0.003	0.003	0.003	0.002**
Paraleptophlebia sp.	0.195*	0.119	0.048	0.108**
Stenonema sp.	0.862***	0.509	0.497	0.885
Filterers				
Parapsyche cardis	0.718*	0.520	0.773**	0.415
Diplectrona modesta	0.471*	0.479	0.357	0.413*
Predators				
Beloneuria sp.	2.207	2.343	0.459	4.740***
Isoperla spp.	0.163***	0.059	0.046	0.059

Note: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Shredders exhibited greater drift densities in the treatment stream during autumn 1996 and autumn 1998 following small and large wood removal, respectively. The proportion of drifting shredders also increased after wood removal. Wood is important to some shredders as a substrate (Benke et al. 1984; Smock et al. 1989) or a food source (Pereira et al. 1982; Wallace et al. 1999) and as a retention device for fine particulate organic matter (Bilby and Likens 1980; Wallace et al. 1995). Fine particulate organic matter likely became an important food source for early instars of shredders in the absence of course particulate material. Except for *Paraleptophlebia* sp. and *Sciara* sp. (Pereira et al. 1982), taxa in the study streams known to feed on wood were not often found in the drift. The mean drift density of *Sciara* and *Paraleptophlebia* over the study period was similar between the reference and treatment streams. Size of *Sciara* individuals in the drift was not different between streams; however, *Paraleptophlebia* were significantly smaller (Mann–Whitney rank sum test, $P = 0.029$) and occurred more often (37 months compared with 18 months) in the drift of the treatment stream

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than in the reference stream. Except for greater shredder densities in the autumn of wood removal years, wood removal had little effect on the composition and abundance of drift in the treatment stream.

Size comparisons of individuals in the drift and benthos

Except for filterers, the majority of common taxa in the drift of the treatment stream showed no size differences with, or were significantly larger than, their benthic counterparts. We suggest that the need for larger food particles in mid- to late instars increased with development, and the reduced number of these large particles induced emigration in search of better food sources. In the reference stream, where most of the common taxa in the drift were smaller than those in the benthos, drift appears to represent a dispersal stage following hatching. Filterers (i.e., *P. cardis* and *D. modesta*) were smaller in the drift of both streams, perhaps because early instars compete for space as a result of clumped distributions of hatchlings (Glass and Bovbjerg 1969). O'Hop and Wallace (1983) found similar results for these taxa in the drift of Hugh White Creek, another Coweeta stream. Therefore, our observations provide additional evidence for the hypothesis that production of *P. cardis* and *D. modesta* may still be more space limited than food limited in the treatment stream.

In summary, our results demonstrate that resource reduction influences the drift of stream invertebrates. Litter exclusion and lower benthic densities resulted in lower drift densities, but the proportion of benthic animals drifting was greater in the treatment stream. Thus, drift may be used as a mechanism by mobile individuals to locate more abundant food resources. This study supports Waters' (1966) hypothesis that in streams, individuals may emigrate as a function of resource availability.

Acknowledgements

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Littoral water temperature response to experimental shoreline logging around small boreal forest lakes

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Abstract: Shoreline logging did not significantly increase average littoral water temperatures in two small boreal forest lakes in northwestern Ontario, Canada. However, over the early summer monitoring period clearcut shorelines were associated with increases of 1–2°C in maximum littoral water temperature, and increases of 0.3–0.6°C in average diurnal temperature range, compared with undisturbed shorelines or shorelines with 30-m shoreline buffer strips. Comparison of simultaneous water temperatures at littoral locations with and without shoreline forest showed that increased temperatures were caused by daytime heating.

Résumé : La coupe de la forêt le long de la rive n'a pas fait augmenter de façon significative la température littorale moyenne de deux petits lacs boréaux dans le nord-ouest de l'Ontario au Canada. Cependant, durant la période initiale d'observation au début de l'été, les rives dénudées étaient associées à un accroissement de 1–2°C de la température maximale de l'eau dans la zone littorale et une augmentation de 0,3–0,6°C de l'étendue moyenne de la température journalière, par comparaison avec des rives non modifiées ou d'autres protégées par une bande tampon de 30 m. Une comparaison des températures mesurées simultanément dans des sites littoraux adjacents à des rives avec et sans forêt riparienne montre que les températures accrues résultent d'un réchauffement durant la journée.

[Traduit par la Rédaction]

Introduction

In streams, shoreline clearcutting and wildfire are unequivocally associated with increased summer water temperature and temperature variability. These impacts are usually attributed to decreased shading, although other local factors including wind, stream discharge, channel form, and groundwater inputs can all be important (Brown and Krygier 1967; Holtby 1988; Johnson and Jones 2000). In lakes, water temperature is influenced by a complex and interacting suite of factors, including air temperature, altitude, direct and indirect solar energy, wind, fetch, water clarity, and depth, with different factors dominating at different locations and different spatial or temporal scales (Mazumder and Taylor 1994; Fee et al. 1996). The relevant physical processes are well understood (Edinger et al. 1968), and good empirical models (based mainly on air temperature and lake morphometry) are available for predictions of whole-lake and littoral water temperatures (Shuter et al. 1983; Matuszek and Shuter 1996; Håkanson 1996). However, little is known about lake temperature response to forest disturbance. A single postlogging comparative study of littoral water temperatures in northwestern Ontario suggested that shoreline clearcutting had limited influence on littoral water temperatures, with daytime temperature increases usually less than 1°C (Steedman et al. 1998).

Shoreline buffer strips (reserves of undisturbed shoreline forest designed to protect lakes and streams from forestry or other land uses) are widely prescribed by boreal forest managers to protect fish habitat and water quality. Preservation of shoreline forest is intended to provide a range of benefits to aquatic habitats, including shade, bank stability, inputs of forest litter, branches, and boles, and retention of sediments and nutrients from upland runoff. Forested shoreline buffer strips of at least 15 m width are generally sufficient to prevent stream temperature increases after logging, but the other benefits have proven more difficult to quantify (Clinnick 1985; Castelle et al. 1994). Riparian buffer strips do not appear to be effective in preventing water quality changes associated with catchment disturbance by logging or wildfire (Norris 1993; Steedman 2000; Carignan et al. 2000).

Selective logging and regeneration of lakeshore forest may become a component of landscape-scale natural disturbance emulation in managed boreal forests. Although wildfire regularly disturbs or destroys forests surrounding boreal forest lakes, there are uncertainties regarding environmental consequences, including water temperature impacts, of lakeshore forest management. The objectives of this study were (*i*) to use available topographic and land-cover information to calculate a first approximation of shade loss associated with shoreline deforestation on small lakes in boreal shield terrain; (*ii*) to measure experimental shoreline forestry impacts on littoral water temperature at annual, daily, and hourly time scales; and (*iii*) to assess the effectiveness of shoreline

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Table 1. Description of study lakes and summary of experimental treatments.

Lake	L26	L42
Location (N lat., W long.)	49°07′15″, 92°08′45″	49°05′00″, 92°09′30″
Nominal experimental treatment	Moderate catchment deforestation, no shoreline deforestation	Extensive catchment and shoreline deforestation
% terrestrial catchment area clearcut (1996, 1996+1998)	33, 45	71, 74
% shoreline length clearcut (1996, 1996+1998)	0, 0	42, 61
No. tributary Lakes	0	0
Max. depth (m)	37	18
Surface area (ha)	29	26
Lake volume (10^5 m^3)	40.8	21.5
Avg. depth	14.1	8.3
Maximum fetch (m) and orientation	900, north–south	1100, north–south
Total catchment area (ha)	106	70
Ratio terrestrial catchment area–lake surface area	2.6	1.6
Water renewal time (years)[a]	13.1	10.5
Average Secchi depth (m)[b]	8.1	6.7
June, Sept. thermocline depth (m)[c]	4.6, 9.3	4.5, 9.5

[a]Based on 1995 to 1997 average local runoff of 0.293 m·year^{-1} (Beaty 1998).
[b]1991 to 1995 May to September average.
[c]1991 to 1995 average (Steedman and Kushneriuk 2000).

buffer strips in preventing potential water temperature increases in littoral waters.

Methods

Study site

The two small headwater lakes monitored in this study (L26 and L42) were located in the Ontario Ministry of Natural Resources' Coldwater Lakes Experimental Watersheds, in boreal – Great Lakes transition forest on the Canadian shield, approximately 200 km northwest of Thunder Bay, Ontario, Canada (Table 1, Figs. 1–3). L26 is located approximately 4 km northeast of L42. The lake catchments had shallow soils with abundant boulders and bedrock outcrops, moderate slopes (15–50%), and relief generally not more than about 60 m. Catchment forests consisted of 75- to 100-year-old fire-origin jack pine (*Pinus banksiana*) stands, with trembling aspen (*Populus tremuloides*), and black spruce (*Picea mariana*), with some paper birch (*Betula papyrifera*), eastern white cedar (*Thuja occidentalis*), red pine (*Pinus resinosa*), and eastern white pine (*Pinus strobus*). The study lakes had similar solute and nutrient content and were extremely dilute, with specific conductance of about 14–22 μS·cm^{-1}, 2–3 mg·L^{-1} dissolved organic carbon, total P of less than 5 μg·L^{-1}, and chlorophyll *a* of less than 2 μg·L^{-1} (Steedman 2000). The lakes contain native populations of lake trout (*Salvelinus namaycush*), white sucker (*Catostomus commersoni*), and 5–7 species of smaller fish species (primarily Cyprinidae, Gasterosteidae, and Etheostomidae).

Description of shoreline logging

The two study lakes received different logging treatments. Between September 1 and October 31, 1996, 33% of the L26 catchment area was clearcut, with at least 30 m of undisturbed forest preserved around the entire shoreline (Fig. 2). Most logging on the L26 catchment was in the southern portion, because of rugged terrain in the northern portion. The 9-ha catchment of an intermittent tributary stream at the south end of L26 was left undisturbed in 1996 and clearcut, except for a 30-m shoreline buffer strip, between June 1 and 20, 1998. This increased L26 catchment deforestation to 45%. Between June 21 and July 31, 1996, 71% of the L42 catchment area was clearcut, including 42% of the shoreline length (Fig. 3). Small areas in the southern and northeastern portions of the L42 catchment were too rugged for logging operations. A temporary 500 × 30 m shoreline buffer strip on the southwest shore of L42 was left undisturbed in 1996 and harvested 2 years later between June 1 and 4, 1998. This increased L42 shoreline deforestation to 61% and catchment deforestation to 74%. Both lakes were logged by commercial operators using a tracked feller buncher, chainsaws, and skidders. Further description of the experimental logging can be found in Steedman and Kushneriuk (2000). Shoreline logging was not associated with significant soil disturbance, and understory shrubs, primarily green alder (*Alnus crispa*), leatherleaf (*Chamaedaphne calyculata*), Labrador tea (*Ledum groenlandicum*), and bush honeysuckle (*Diervilla lonicera*), were left intact in the riparian zone.

Littoral shade model

A detailed digital elevation model of the L42 catchment and forest canopy was created by merging elevation data from 1 : 20 000 scale Ontario Base Maps, custom aerial photogrammetry, SPOT 3 (Satellite Pour l'Observation de la Terre) satellite imagery of the 1996 clearcuts, and GPS (global positioning system) generated bathymetry and terrestrial feature identification. Based on this terrain model, L42 summer-average direct solar radiation (kw·m^{-2}, May 1 to October 31) was modeled in the ArcView geographic information system. Solar angle and littoral shade loss calculations were based on cloudless skies and simulated removal of an opaque forest canopy 20 m high.

Water temperature monitoring

Littoral water temperatures were monitored in four consecutive years (1995–1998). The annual monitoring period varied somewhat from year to year, but continuous records from June 7 to July 29 (53 days) were obtained in all 4 years at most locations and were used for interyear comparisons. Monitoring began about 1 month after ice-out and always included the time of highest annual water temperature (Fig. 4).

Three shoreline treatments were contrasted between and within years: undisturbed (no logging within 90 m of the water's edge); buffered (clearcut to within 30 m of the water's edge); and clearcut (all merchantable timber removed from the shoreline). Specified shoreline treatments were present for at least 50 m on either side of each monitoring location. 1996 was a prelogging year for L26, as

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Fig. 1. Map of study area showing locations of L26 and L42 in northwestern Ontario.

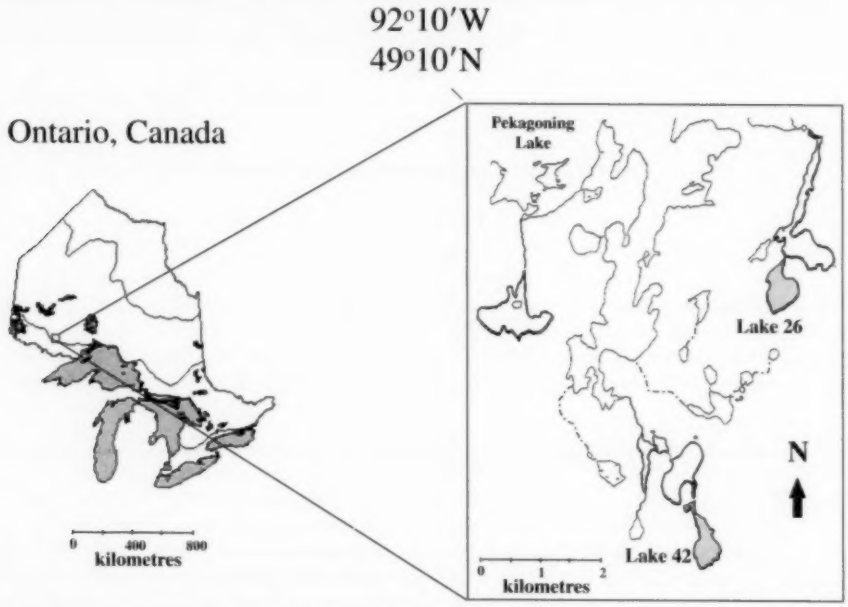
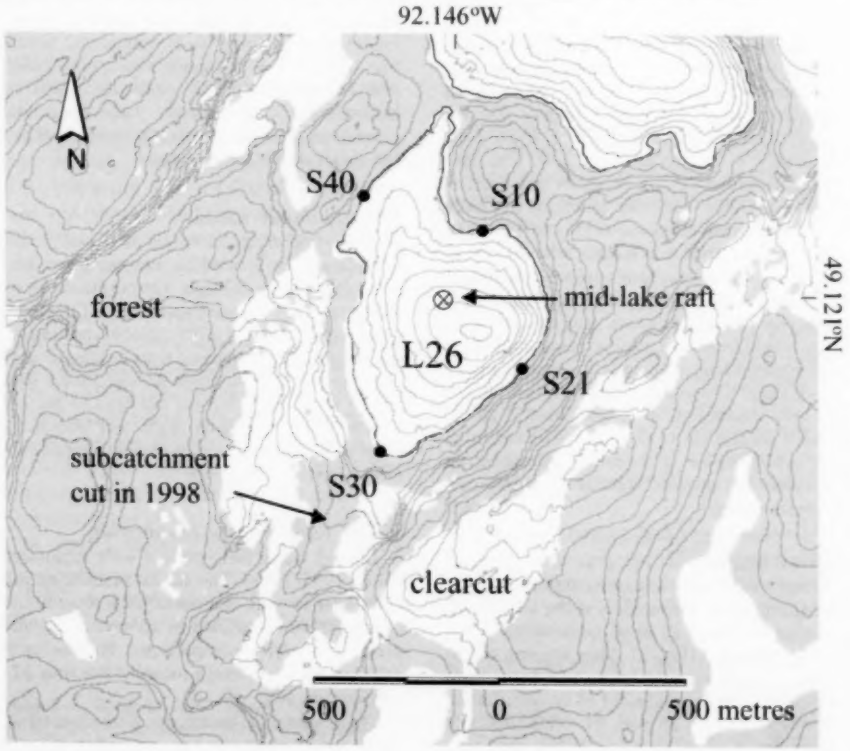


Fig. 2. Map of L26 and surrounding terrain, showing 5-m topographic and bathymetric contours, littoral monitoring locations, and other features mentioned in the text. Undisturbed forest is shown as grey, and clearcuts are shown as white.



logging began in September of that year, after the annual littoral monitoring period. In 1997 and 1998, L26 provided examples of undisturbed and buffered shorelines. Logging in 1996 on L42 progressed around the lake during the monitoring period. In 1997 and 1998, L42 provided examples of buffered and clearcut shorelines. The temporary shoreline buffer strip in place on the southwest shore

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Fig. 3. Map of L42 and surrounding terrain, showing 5-m topographic and bathymetric contours, littoral monitoring locations, and other features mentioned in the text. Undisturbed forest is shown as grey, and clearcuts are shown as white. Legend refers to shading on L42 surface and shows calculated percentage increase in average May to October lake surface solar energy, after 1996 logging.

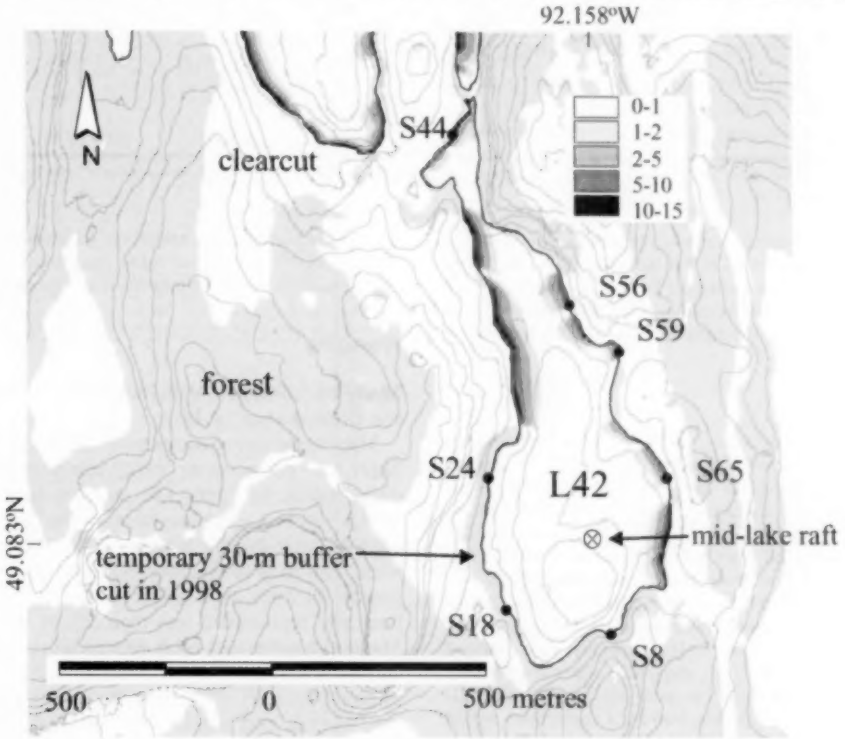
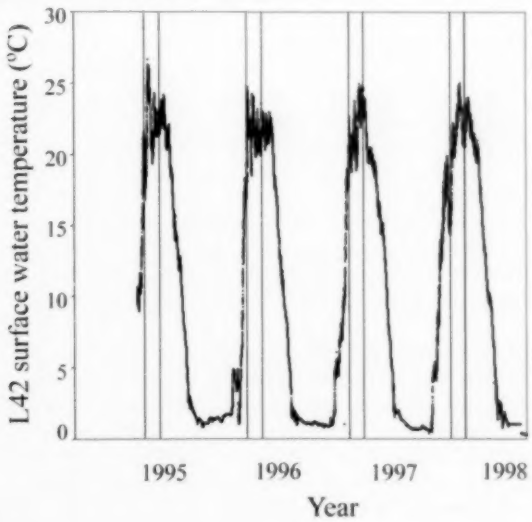


Fig. 4. L42 mid-lake surface water temperature from spring 1995 to fall 1998, with vertical reference lines showing the June 7 – July 29 monitoring periods in each year.



of L42 in 1997 allowed sequential contrasts of undisturbed, buffered, and clearcut treatments at the same location from 1995 to 1998.

Littoral water temperatures were recorded at 15-min intervals by Onset Stowaway temperature recorders in buoyant "subcase" housings with embedded thermistors. Because of logistic uncertainties associated with the commercial logging operation, the timing and pattern of shoreline logging (particularly clearcut shoreline locations on L42) could be specified only approximately at the beginning of this study in 1995. We therefore deployed our limited stock of temperature recorders in locations representing a range of shoreline aspects and bathymetry. The same recorders were placed at the same locations (identified by "sector number" signs, e.g., S24) in all years of the study, around the main basin of each lake and in additional locations on L42 (in an isolated embayment and along the planned temporary shoreline buffer), in areas free of macrophytes and large wood debris (Figs. 1, 2). Two recorders were added to L42 in 1996, on the east and west shores. Positioning of recorders was standardized as much as possible by mooring them 0.3–0.5 m deep, 1–3 m from the water's edge, in about 0.7–1.0 m of water. Two recorders failed during the study; one failed during 1995 monitoring on L26, and one during 1998 monitoring on L42. Temperature sensors in the littoral recorders were accurate to within 0.2°C in a 5-day enclosure comparison trial. All temperature data were aggregated to hourly averages before analysis

Offshore gradients of littoral water temperature were measured during the 1998 monitoring period at S18 on the southwest shore of L42, a clearcut location with moderate bathymetric slope (Fig. 3). Seven temperature loggers were moored in a transect perpendicular to shore, arrayed 0.5 m below the surface and 0.5 m above the lake bottom, in water depths of 1, 2, 3, and 4 m, 3–15 m from shore. These recorders were in addition to the S18 recorder deployed nearby for the main experiment.

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Table 2. Average water temperature (°C) for June 7 to July 29, 1998, and diurnal temperature range (°C, in parentheses) along an offshore transect at S18, L42.

	Offshore distance (m)				
Recorder depth (m)	3	8	11	15	200 (mid-lake raft)
0.5	20.6 (1.3)	20.7 (1.1)	20.8 (1.1)	20.7 (1.0)	21.1 (0.9)
1.5		20.5 (1.0)			
2.5			20.4 (0.9)		
3.5				20.0 (0.7)	20.6 (0.6)

Note: Total water depth was 0.5 m greater than recorder depth, except at the mid-lake station where total water depth was 18 m.

Mid-lake air and epilimnetic water temperatures (at depths of 0.5 m and 3.5 m) were measured at 5-s intervals from May 1995 through September 1999, by a Campbell Scientific data logger and sensors mounted on rafts near the middle of the main basin of each lake. Temperature sensors on the rafts were nominally accurate to 0.2°C.

Data analysis

This study compares continuous, replicated water temperature measurements from the various shoreline treatments, at annual, daily, and hourly time scales. The data had approximately normal distributions and were not transformed. With certain exceptions, standard parametric statistical techniques (e.g., analysis of variance) were inappropriate and were not required for quantification of treatment effects. The temperature measurements used in this study were sequential at an arbitrary but regular interval (i.e., the data are a "census" rather than a random sample), and they show a high degree of temporal and spatial autocorrelation as a result of thermal inertia and lake mixing (i.e., sequential water temperature measurements from different shoreline locations are not independent observations). Use of parametric statistical techniques would require specification of a very high and meaningless sample n, leading to gross underestimates of variance. All statistical analyses were conducted on SPSS version 9 for Windows.

Annual average (with 95% distribution limits) and maximum water temperatures for the 1995–1998 monitoring periods are presented in tabular form for each littoral and mid-lake monitoring location. These are exact values (within the limits of the instrumentation) and may be directly compared between years and locations. Annual littoral temperature means and maxima are illustrated in box–whisker plots to show central tendency, annual variation, and treatment effects.

Diurnal water temperature ranges at littoral locations before (1995) and after (1997, 1998) logging did not show significant temporal autocorrelation and were compared in an analysis of covariance. Mid-lake 0.5 m diurnal water temperature range was used as a covariate to account for daily and annual weather patterns that otherwise completely obscured shoreline treatment effects. Annual covariate regressions (i.e., littoral diurnal temperature range as a function of mid-lake diurnal temperature range) were specified for each littoral location and were always highly significant ($p < 0.001$), with r^2 of 0.6–0.8, slopes of 0.9–1.0, and intercepts of 0.6–0.7°C. Treatment impacts were estimated for covariate average values of 1.0°C for L26 and 1.1°C for L42 (i.e., the estimates represent impacts on "average" days when mid-lake diurnal temperature range was about 1°C). Bonferroni adjustment was used for all post-hoc contrasts.

Hourly impacts of shoreline treatments were examined on L42 as the hourly temperature difference between pairs of shoreline locations during the day (07:00–21:00 central standard time) when solar heating could be expected and at night (22:00–06:00) in the absence of solar heating. Box–whisker plots were used to illustrate the distributions of hourly temperature differences. These plots illustrate L42 within-lake treatment contrasts available in each year of the study. The realized study design did not allow all possible contrasts of shoreline treatments and aspects.

Results

Modeled influence of deforestation on solar energy in the littoral zone of L42

Map-based calculations provided a first approximation of likely L42 littoral solar energy increases after 42% shoreline deforestation in 1996. The analysis indicated that most of the L42 surface experienced a relatively small amount of additional solar energy after 1996 shoreline logging (Fig. 3). Simulated May to October average solar energy increases of greater than 5% were restricted to waters off clearcut shorelines and represented less than 5% of the lake surface area. Maximum estimated solar energy increases of 10–15% were indicated up to 10 m from shore at these locations. These calculations refer to the specific conditions of lake morphology, terrain, and logging that applied to L42 in 1996 and would not be quantitatively applicable to other lakes. For example, a long, narrow lake (less than about 30 m wide) oriented east to west would have a higher proportion of its surface area shaded by shoreline forest. However, the offshore extent of shade shown in Fig. 2 should be representative of lakes in the region.

This landscape scale model was not designed to estimate local shade losses associated with our littoral temperature monitoring locations. Shade associated with residual patches of shoreline forest on the clearcut eastern shore of L42 (near S56 and S59) was probably exaggerated by the model. These patches were classified as intact forest canopy by the image classification algorithm we used to interpret the SPOT satellite image but were too small and sparse to provide effective littoral shade. Steep terrain and the southerly viewing angle of the SPOT satellite also obscured some narrow clearcut areas along the south shore of L42, just southwest of S8.

Offshore gradients in littoral water temperature

Average water temperature and diurnal temperature range varied with offshore distance and depth during the 1998 monitoring period at S18 on L42 (Table 2). Average nearshore water temperatures at a depth of 0.5 m did not vary by more than 0.2°C within the nearshore transect but averaged about 0.5°C lower than at mid-lake. Mean diurnal temperature range at a depth of 0.5 m was highest near shore and declined with offshore distance from 1.3°C at 3 m from shore to 0.9°C at the mid-lake raft. Both mean temperature and daily range declined with depth, with average nearshore

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Table 3. Average early-summer air, mid-lake surface water, and littoral water temperatures (°C) for June 7 – July 29, 1995–1998, with 95% distribution interval in parentheses, followed by maximum temperature observed in the monitoring period.

			Year		
Lake	Location	Shoreline treatment 1995 to 1998	1995 (prelogging)	1996	1997	1998
L26	Air (mid-lake raft)		19.0 (7.7, 30.3) 35.3	17.8 (8.5, 27.1) 31.1	18.5 (8.9, 28.2) 30.0	18.3 (10.1, 26.5) 30.7
	Mid-lake (0.5 m)		22.0 (17.9, 26.1) 26.3	20.8 (17.8, 23.8) 23.3	21.5 (18.2, 24.7) 24.9	21.2 (16.3, 26.0) 24.7
	S10 (northeast)	U U U U	Recorder failed	20.9 (17.6, 24.1) 24.5	21.4 (18.1, 24.7) 25.4	21.0 (16.2, 25.8) 25.0
	S21 (southeast)	U U U U	21.9 (17.8, 26.0) 26.7	20.7 (17.5, 24.0) 24.4	21.3 (17.8, 24.7) 25.5	20.8 (15.9, 25.7) 24.6
	S30 (southwest)	U U B B	21.8 (17.7, 25.9) 27.2	20.5 (17.2, 23.8) 24.3	21.1 (17.7, 24.5) 25.8	20.7 (15.7, 25.6) 24.7
	S40 (northwest)	U U U U	21.9 (17.7, 26.1) 26.7	20.7 (17.5, 23.9) 24.1	21.4 (17.9, 24.9) 25.3	20.9 (16.1, 25.7) 24.7
L42	Air (mid-lake raft)		19.0 (8.1, 29.9) 35.0	17.8 (8.9, 26.7) 30.7	18.6 (9.3, 27.8) 29.7	18.3 (10.5, 26.1) 30.3
	Mid-lake (0.5 m)		21.8 (17.5, 26.0) 26.6	21.1 (18.3, 24.0) 24.7	21.4 (18.2, 24.6) 24.9	21.1 (16.2, 26.0) 25.0
	S44 (northwest, bay)	U UC C C	22.1 (17.3, 26.9) 27.9	20.7 (17.1, 24.3) 24.9	21.5 (17.7, 25.3) 27.1	20.9 (15.8, 26.0) 26.7
	S56 (northeast	U UC C C	21.7 (17.3, 26.1) 26.6	20.5 (17.2, 23.8) 24.6	21.2 (17.7, 24.8) 25.6	20.8 (15.8, 25.8) 25.9
	S59 (east)	U UC C C	21.9 (17.5, 26.3) 27.1	20.5 (17.1, 24.0) 24.4	21.4 (17.7, 25.1) 26.4	Recorder failed
	S65 (east)	U UC C C	Not deployed	20.6 (17.2, 24.0) 24.7	21.4 (17.8, 24.9) 25.9	20.9 (15.7, 26.2) 26.0
	S8 (southeast)	U UB B B	21.8 (17.5, 26.1) 27.2	20.4 (17.1, 23.8) 24.7	21.2 (17.7, 24.6) 25.2	20.6 (15.5, 25.7) 25.3
	S18 (southwest)	U UB B C	Not deployed	20.4 (17.1, 23.7) 24.5	21.1 (17.7, 24.5) 24.8	20.7 (15.6, 25.8) 25.1
	S24 (west)	U UB B C	21.6 (17.4, 25.9) 26.7	20.3 (17.1, 23.5) 23.7	21.0 (17.7, 24.3) 24.7	20.7 (15.6, 25.7) 24.9

Note: Shoreline forest condition in each year is coded as follows: U = undisturbed; B = buffer strip; and C = clearcut to shore. Double codes for 1996 indicate that logging occurred during the June 7 – July 29 monitoring period.

Fig. 5. Boxplots showing data distributions of littoral temperature means (*a*) and maxima (*b*) at undisturbed (open boxes), buffered (gray boxes), and clearcut (solid boxes) shoreline treatments in the 1995–1998 monitoring periods. Data from both lakes are pooled in these plots. Horizontal lines forming the bottom, middle, and top of each box represent the 25th, 50th, and 75th percentiles of each set of observations, respectively. The vertical lines at the bottom and top of each box extend to the values of the minimum and maximum observations. The number of locations represented by each box is listed along the bottom of each figure.

water temperatures at 3.5 m deep up to 0.7°C cooler than water at 0.5 m deep.

Average and maximum littoral water temperatures

Before logging, the two study lakes had similar average littoral water temperatures, with a maximum difference between littoral locations of 0.5°C (Table 3). Shoreline location appeared to have some influence on littoral water temperature, but this was also influenced by lake morphology. On L26, the northern station was usually the warmest, and the southern station was usually the coolest, by a few tenths of a degree. The eastern and western shorelines had intermediate and nearly identical average temperatures. Al-

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Table 4. Average June 7 to July 29 diurnal water temperature range (°C) at littoral monitoring locations before (1995) and after (1997, 1998) logging treatments.

Lake	Location	Prelogging (1995) mean	Shoreline forest 1997, 1998	Mean difference after logging 1997	1998
L26	S21	1.4 (1.3, 1.5)	U U	0.3 (0.1, 0.5)*	–0.0 (–0.2, 0.2)
	S30	1.4 (1.3, 1.5)	B B	0.4 (0.2, 0.7)*	0.1 (–0.1, 0.4)
	S40	1.4 (1.4, 1.5)	U U	0.2 (0.0, 0.4)*	0.0 (–0.2, 0.2)
	Littoral average	1.3 (1.2, 1.4)		0.3 (0.2, 0.5)*	0.0 (–0.1, 0.2)
L42	S8	1.7 (1.6, 1.8)	B B	0.2 (0.0, 0.4)*	–0.1 (–0.3, 0.1)
	S24	1.4 (1.3, 1.5)	B C	0.0 (–0.1, 0.2)	0.3 (0.1, 0.5)*
	S44	2.0 (1.8, 2.1)	C C	0.4 (0.1, 0.6)*	0.6 (0.3, 0.9)*
	S56	1.4 (1.3, 1.5)	C C	0.4 (0.2, 0.6)*	0.3 (0.1, 0.5)*
	S59	1.7 (1.6, 1.8)	C C	0.5 (0.2, 0.7)*	Recorder failed
	Littoral average	1.5 (1.4, 1.6)		0.2 (0.1, 0.3)*	0.3 (0.1, 0.4)*

Note: 95% confidence intervals are in parentheses. Postlogging shoreline forest condition is coded as follows: U = undisturbed; B = buffer strip; and C = clearcut to shore. Double codes for 1996 indicate that logging occurred during the June 7 – July 29 monitoring period. n = 52 days· year^{-1}. Means and differences were estimated by analysis of covariance, with mid-lake 0.5 m daily water temperature range as a covariate (see text). Estimates for littoral average were calculated from hourly averages of littoral stations, omitting S59 on L42. Asterisks identify differences where the 95% confidence interval does not span zero.

though the highest average and maximum water temperatures were recorded at S44, in a shallow bay at the north end of L42, the influence of aspect was otherwise not as consistent on L42.

After logging, average and maximum littoral water temperatures never exceeded those observed in 1995 (Fig. 5). Clearcut shorelines generally did not have the highest average temperatures (Fig. 5*a*) but always had the highest maximum temperatures in each annual monitoring period, with annual maxima up to about 1.8°C higher than at undisturbed shorelines (Fig. 5*b*). Buffered shorelines averaged about 0.2–0.3°C cooler than undisturbed shorelines (Fig. 5*a*). In 1997 and 1998, average temperatures at clearcut shorelines on L42 were 0.2–0.3°C higher than at buffered shorelines (Table 3). This was equivalent to about 10–16 degree-days over the monitoring period. However, these differences were similar to average temperature differences between undisturbed shorelines in 1995. A standardized comparison based on the same three stations in each lake (S21, S30, and S40 on L26 and S56, S8, and S24 on L42), representing east, south, and west shorelines, showed that the average littoral temperature in L26 was about 0.2°C higher than in L42 in 1995 and 1996 but that this had declined to about a 0.1°C difference in 1997 and 1998.

Diurnal variation of littoral water temperature

Prelogging diurnal temperature range at littoral locations varied from near zero to about 3.5°C and averaged 0.3°C (L26) to 0.4°C (L42) greater than at mid-lake (Table 4). In 1997, littoral diurnal temperature range increased by 0.2–0.5°C (relative to 1995) at most locations on both L26 and L42. These increases were significant regardless of shoreline treatment but were highest on clearcut shorelines. In 1998, only clearcut L42 littoral locations showed significant increases (0.3–0.6°C) relative to 1995.

Hourly contrasts of L42 shoreline treatments

Before logging, concurrent daytime temperature differences of up to 1°C or more frequently occurred between littoral locations in L42 (Figs. 6*a*–6*d*) and in L26 (not shown), although median differences over annual monitoring periods were generally only a few tenths of a degree. On L42, clearcut shorelines were associated with daytime increases of about 0.2°C in median hourly temperature difference relative to undisturbed or buffered shorelines (Figs. 6*b*–6*d*). Clearcutting increased maximum daytime temperature differences relative to uncut or buffered shorelines by up to 1°C at some locations (e.g., S44, S56, Figs. 6*a*, 6*b*). These effects were strongest in 1997 and 1998 but were also evident at some locations in 1996, when experimental clearcutting occurred during the monitoring period (e.g., S56, Figs. 6*b*, 6*d*). Differences between a clearcut and buffered shoreline observed in 1997 disappeared when the buffered shoreline was clearcut in 1998 (Fig. 6*d*). Examination of the hourly data series showed that littoral water temperatures were highest in the afternoon from about 15:00 to 17:00. At night, the median temperature difference between sites was generally near zero, with maximum differences of about 0.5°C, and treatment effects were not apparent (Figs. 6*a*–6*d*).

Discussion

Littoral waters are part of the epilimnion of these small, stratified lakes but have some unique thermal characteristics associated with their shallow depth, close association with bottom substrates, proximity to shoreline shade and shelter, and potential for reduced mixing with the main body of the epilimnion. These physical factors allow littoral waters to respond faster than mid-lake waters to changing meteorological conditions, including solar energy (Edinger et al. 1968). Our map-based calculations suggested that shoreline clearcutting of small boreal shield lakes could increase nearshore summer-average solar energy by up to 15%. The empirical temperature data presented in this study are consistent with this prediction and demonstrate the occurrence of small, local increases in littoral water temperature during the daytime. Compared with streams, lakes have higher thermal mass and smaller edge–area ratio, and in all but the smallest

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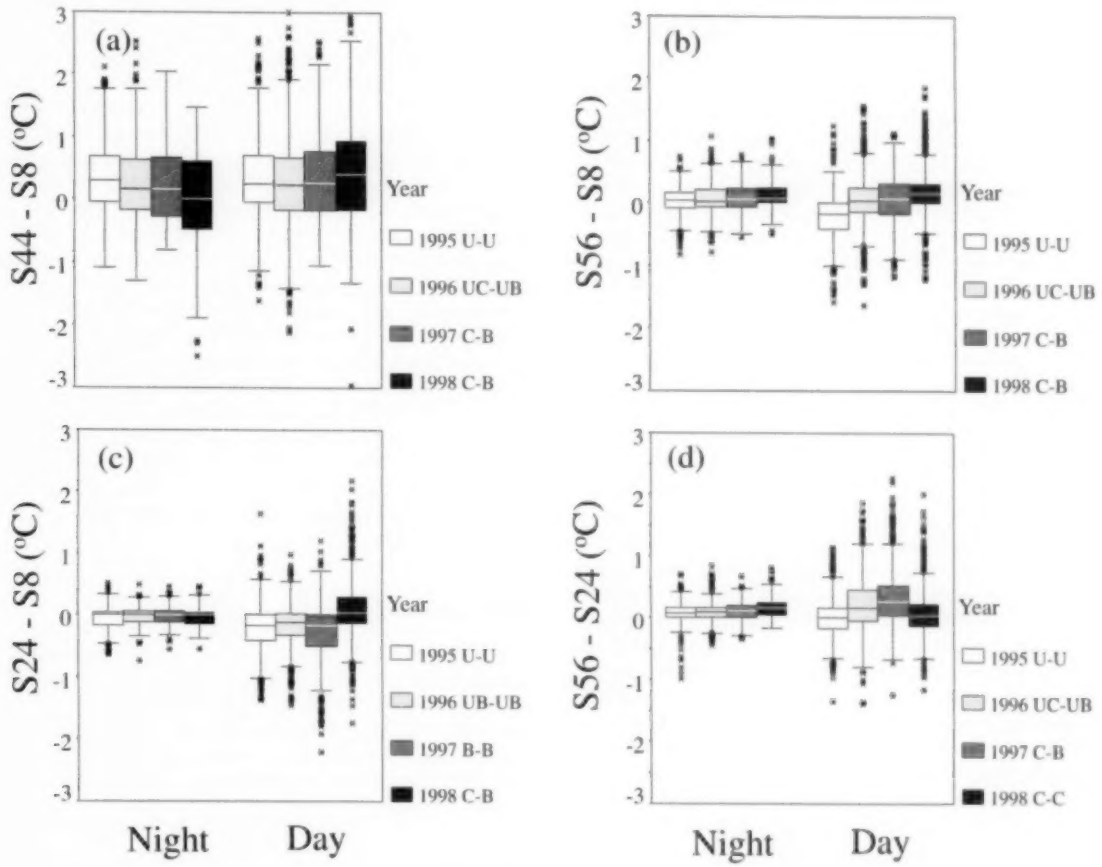
Fig. 6. Distributions of hourly littoral water temperature differences between selected clearcut, buffered, and undisturbed shorelines on L42, aggregated for nighttime (22:00 to 06:00) and daytime (07:00 to 21:00) periods, June 7 – July 29, 1995 to 1998. Shoreline forest treatments are coded as follows: U = undisturbed; B = buffer strip; and C = clearcut to shore. Double codes for 1996 indicate that logging occurred during that June 7 – July 29 monitoring period. For example, "S44–S8" means that S8 average hourly temperatures were subtracted from S44 average hourly temperatures. Likewise, "C–B" means that the plot depicts the difference between clearcut and buffered shoreline treatments at those locations in that year. Horizontal lines forming the bottom, middle, and top of each box represent the 25th, 50th, and 75th percentiles of each set of observations, respectively. The vertical lines at the bottom and top of each box extend 1.5 box-lengths from the 25th or 75th percentile. Asterisks show all extreme observations, except for panel *a*, which had a small number of observations greater than +3°C and less than –3°C. The number of hourly observations represented by each box is 477 and 795 for night and day, respectively.



lakes only a portion of the lake surface may be shaded by shoreline forest. Littoral temperature impacts reported here were much smaller than those reported from studies of stream deforestation, where increases of up to 10°C in maximum temperature of cold-water streams have been reported (Belt et al. 1992). The temperature impacts observed at the study lakes could be expected to last at least 20 years, the minimum time required to re-establish a forest canopy in northwestern Ontario.

Littoral water temperature responses to shoreline clearcutting were generally transient, less than 1°C in magnitude, smaller than observed diurnal and interannual temperature variation, and did not include temperature extremes unprecedented in the study period. In spite of our attempt to statistically remove variation associated with weather, analyses of diurnal temperature ranges indicated significant increases at undisturbed shorelines on L26 between 1995 and 1997. It is likely that this result was associated with some aspect of 1997 littoral heating not captured by the mid-lake water temperature covariate. Although this suggests that significant impacts observed on L42 in 1998 could be spurious, this is not supported by the consistent pattern of impacts in 1998, nor by the within-lake hourly contrasts. Consistent temperature impact estimates were obtained from different analyses of logging impacts at small time scales. Both the analysis of covariance of 1998 diurnal temperature range and the plots of median hourly daytime temperature difference between clearcut and forested shorelines suggested that

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logging impacts of a few tenths of a degree frequently occurred and that increases of 0.5°C or more occasionally occurred. Littoral temperature increases were significant only during daytime hours (usually in late afternoon) and did not produce detectable changes in long-term average temperature. As was reported for a postdisturbance comparative study of nearby lakes (Steedman et al. 1998), this experimental study also suggests that littoral degree-day accumulation would not be altered significantly by shoreline logging. The only significant difference in annual average temperature was seen at buffered shorelines, which averaged about a quarter of a degree cooler than undisturbed sites. This could have been associated with increased wind exposure through the 30-m buffer strip and increased frequency and intensity of littoral mixing. However, if this occurred, it should have been more intense on clearcut shorelines, which did not show such declines in average temperature. It is possible that there were compensatory interactions of wind and solar heating on clearcut shorelines, over the monitoring period. At the whole-lake scale, mid-lake wind velocity, spring and fall circulation efficiency, stratification duration, thermocline depth, and epilimnetic water quality were not altered significantly by clearcut logging around the lakes during the period of this study (Steedman and Kushneriuk 2000; Steedman 2000).

Our data suggest, but do not demonstrate, that daily timing and spatial pattern of littoral solar heating would also change after shoreline logging. Postlogging solar heating of littoral waters will be greatest during those times of the day when a shoreline would formerly have been shaded by shoreline forest (e.g., in the afternoon on a western shoreline). On cloudy days, heating associated with shoreline deforestation will be reduced or eliminated. The largest impacts would be expected on southern shores that had little shading associated with topographic relief. Because of rugged terrain on the south shore of L42, the present study did not include a south shoreline clearcut and may underestimate potential impacts on south shore littoral water temperatures. However, the maximum littoral water temperature impacts observed in this study were similar to those reported by Steedman et al. (1998) for a south shore clearcut.

Water temperatures during this study were representative of recent years. Although the 1995 prelogging "reference" year had unusually hot weather in early June 1995, L42 May–September average surface water temperature (18.7°C) was exceeded in 1996 (19.6°C) and 1998 (19.3°C). The coolest year of this study was 1997 (17.5°C). Extreme values of this temperature index in the last decade occurred in 1991 (20.8°C) and 1992 (16.2°C) (Steedman and Kushneriuk 2000). This study reports temperatures for early summer, when littoral waters were warming. Although annual patterns varied considerably between years, lake waters were generally cooling by the end of July. Monitoring records available from 1995 showed that littoral stations cooled faster than mid-lake locations in the second half of the summer. It is unlikely that seasonal extremes in littoral water temperature occurred after July 29.

Although it is possible that logging impacts on large tributary streams could influence littoral water temperatures, this probably did not occur on the study lakes. These were headwater lakes that did not have large channelized inflows (L42 is fed entirely by subsurface runoff). S30 on L26 was 10 m east of a small inflow stream (9 ha catchment, discharge of about 3 $L \cdot s^{-1}$) that was clearcut before the 1998 monitoring interval and showed postlogging temperature increases of up to 6°C (C. Allan, University of North Carolina at Charlotte, Charlotte, N.C., U.S.A., unpublished data). Temperatures at S30 in 1998 showed no evidence of heating from the tributary, relative to the other littoral locations that were monitored.

Average water temperature changes of 2–4°C have been shown to affect detrital decomposition, primary production, invertebrate growth (Webster and Waide 1982; Rempel and Carter 1986, 1987), and fish behaviour and production (Bardach and Bjorklund 1957; Meisner et al. 1987; Holtby 1988). Annual growth increments of young smallmouth bass in Lake Opeongo, Ontario, were estimated to change by about 4 mm for every 1°C change in summer-average epilimnetic water temperature (King et al. 1999). Biota inhabiting the littoral zones of the study lakes must cope with water temperatures that vary annually from about 1 to 28°C, with daily variation of 0–3°C, light conditions from full shade to full sunlight, and frequent onshore winds. Partial catchment and shoreline deforestation by wildfire probably occurred historically at intervals of not more than 100 years in this region of the boreal forest, although fire frequency has declined significantly in recent decades owing to fire suppression (Li 2000). It is not likely that the changes in maximum and average temperature associated with temporary shoreline deforestation will have significant life history or behavioural implications for littoral biota in these lakes. However, measurements of postlogging habitat and biota in these lakes are not yet complete.

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A hierarchical Bayesian model for estimating historical salmon escapement and escapement timing

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Abstract: In this paper, we present an improved methodology for estimating salmon escapements from stream count data. The new method uses a hierarchical Bayesian model that improves estimates in years when data are sparse by "borrowing strength" from counts in other years. We present a model of escapement and of count data, a hierarchical Bayesian statistical framework, a Gibbs sampling approach for evaluation of the posterior distributions of the quantities of interest, and criteria for determining when the model and inference are adequate. We then apply the hierarchical Bayesian model to estimating historical escapement and escapement timing for pink salmon (*Oncorhynchus gorbuscha*) returns to Kadashan Creek in Southeast Alaska.

Résumé : On trouvera ici une méthodologie améliorée pour estimer les échappées de saumon à partir des données de dénombrement dans un cours d'eau. La nouvelle méthode utilise un modèle hiérarchique bayésien (HBM) qui améliore les estimations pour les années où les données sont rares en " empruntant de la puissance " aux dénombrements des autres années. Nous présentons un modèle pour les données d'échappées et de dénombrement, un cadre statistique hiérarchique bayésien, une stratégie d'échantillonnage de type Gibbs pour l'évaluation des distributions a posteriori des valeurs recherchées et des critères pour déterminer quand le modèle et les inférences sont adéquats. Nous appliquons le modèle HBM à l'estimation des échappées des années antérieures et du moment des retours des Saumons roses à Kadashan Creek dans le sud-est de l'Alaska.

[Traduit par la Rédaction]

Introduction

Escapement data are essential for salmon population conservation and management (Quinn and Deriso 1999). In North America, most escapement data are obtained by aerial or foot escapement surveys (Cousens et al. 1982) in which fish observed in a stream are enumerated at several occasions to obtain a series of counts. Each count is just an estimate of the actual number of spawners in a stream at the time of the survey, not the total escapement (some fish will have died before counting and some will not yet have entered). Thus, some method must be used to convert these counts to escapement. Usually, escapement is estimated with the "area-under-the-curve" method (English et al. 1992; Hilborn et al. 1999), a somewhat ad hoc calculation that uses the counts in conjunction with an estimate of the average longevity of spawners (stream life) (Perrin and Irvine 1990; Fukushima and Smoker 1997). More recently, statistical models have been developed to estimate escapement from escapement counts. Quinn and Gates (1997) developed a biologically detailed stream escapement model to estimate salmon escapement dynamics. Hilborn et al. (1999) provided a maximum likelihood method to estimate stream escapement using a simpler model. In addition to providing an estimate of the total escapement, these statistical methods can estimate escapement timing as well. Escapement timing information is an important prerequisite for run reconstruction techniques (Starr and Hilborn 1988).

For these modeling approaches, separately estimating the escapement in each year may be adequate for years with informative data (Quinn and Gates 1997; Hilborn et al. 1999). However, in some years, counts may be sparse and insufficient to provide reliable estimates. Even with a large number of survey counts, estimation can easily fail due to a lack of data for the last half of the run (Hilborn et al. 1999). Area-under-the-curve estimates are even more affected by such holes in the data, as part of the curve is missing. Such deficiencies are common in historical data; weather, human resource shortages, or budget difficulties may limit counts, and managers often discontinue counts once escapement goals are met.

Hilborn et al. (1999) proposed using prior information on run timing to constrain the escapement model when data for a particular year were uninformative. Such information is most logically derived from the escapement timing of the stock in other years. The timing of salmon returning to a particular stream is remarkably consistent from year to year (Heard 1991), so historical data may contain strong prior information on escapement timing in the current year. One could specify prior distributions for escapement timing parameters from this historical information and perform a

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Bayesian or even a maximum likelihood analysis separately for each year of data (Hilborn et al. 1999). A more formal statistical methodology, hierarchical modeling (Lindley and Smith 1972; Gelman et al. 1995), exists that would allow estimation for all years simultaneously, "borrowing strength" from years with informative data to improve estimates for years with uninformative data.

Hierarchical modeling has many applications in biology, medicine, economics, etc. (Davidian and Giltinan 1995; Gelman et al. 1995). It is also naturally applied in meta-analysis where studies have to be pooled together (Mosteller and Chalmers 1992; for a fisheries example, see Liermann and Hilborn 1997). Hierarchical models assume dependence among parameters, with parameters in lower levels regarded as samples drawn from higher-level population distributions.

Compared with nonhierarchical approaches, one advantage of hierarchical models is that they make full use of all of the data available and can estimate parameters at all levels simultaneously. Another advantage of hierarchical modeling is that it saves degrees of freedom by structuring some dependence among the parameters, reducing the effective number of parameters and thereby avoiding problems of overfitting that are often suffered by nonhierarchical models (Gelman et al. 1995). Bayesian (Gelman et al. 1995; Carlin and Louis 1996) and traditional maximum likelihood procedures (Davidian and Giltinan 1995) can both be applied for the fitting of hierarchical models, although the Bayesian approach provides more accurate assessments for uncertainty in parameters (Browne and Draper 2000).

In this paper, we develop a statistical escapement estimation methodology using hierarchical Bayesian modeling (HBM). The hierarchical component is the assumption that the timing of escapement in each year is a sample drawn from a stock-specific distribution of possible timings. This assumption enables us to use all of the historical survey data for a stream to improve escapement estimates for years with uninformative data as well as to make inferences about typical escapement characteristics of the stream.

We also incorporate an additional improvement over past escapement estimation practices. Traditional methods, such as the area-under-the-curve method and Hilborn et al.'s (1999) model, used an average stream life to convert counts to escapement. However, it is well known that longevity of salmon on the spawning ground declines as the season progresses (Dangel and Jones 1988; Perrin and Irvine 1990; Fukushima and Smoker 1997), so using an average stream life may bias the estimation. Our spawning abundance model incorporates a stream life that declines as the season progresses.

The article is organized as follows. First, we describe a salmon spawning abundance model. We then develop an HBM that combines counts for all of the years together. A hybrid Metropolis–Gibbs algorithm is used for fitting the HBM. We derive the full conditional distributions needed for this approach. We demonstrate a whole set of Bayesian methodologies for high-dimensional Bayesian model fitting through Markov chain Monte Carlo (MCMC) techniques (Gilks et al. 1996), detailed convergence diagnostics of MCMC (Appendix B), and Bayesian model checking and comparison (Appendix C). Finally, we apply the HBM approach to escapement estimation for a pink salmon (*Oncorhynchus gorbuscha*) stock in Southeast Alaska.

Models and methods

A salmon spawning abundance model

There are two processes determining the dynamics of salmon spawning abundance in a stream during the spawning season: entry and mortality. Let η_t denote the number of spawners at the beginning of day t, x_t the number of spawners entering the stream during day t, and d_t the number of fish that die in the same period; then the spawning abundance is

$$(1) \qquad \eta_{t+1} = \eta_t + x_t - d_t = \sum_{k=1}^{t} x_k - \sum_{k=1}^{t} d_k$$

with an initial condition $\eta_{T_1} = 0$ at the starting day T_1 of the stream entry.

Weir studies show that salmon escapement timing can be asymmetric, with pulses of stream entry. With infrequent stream counts, it is usually intractable to estimate these irregular features of stream entry. To some extent, these irregularities in entry are smoothed in taking stream counts by the overlap of fish that arrived on multiple days. In our model, the daily entry of salmon into the stream is approximated by a normal curve:

$$(2) \qquad x_t = E e^{-(t-M)^2/(2S^2)} / \Psi$$

where E denotes the total escapement, M denotes the mean date of arrival, and S denotes the standard deviation of the dates of arrival (i.e., the duration of the run). The value

$$\Psi = \sum_{t=T_1}^{T_2} e^{-(t-M)^2/(2S^2)}$$

is a normalizing constant ensuring that

$$\sum_{t=T_1}^{T_2} (e^{-(t-M)^2/(2S^2)} / \Psi) = 1$$

so that daily entry takes certain percentage of the total escapement. The value T_2 represents the last day of the stream entry.

We add one level of biological realism not usually incorporated in escapement models. Let $l(t)$ be the stream life of the fish entering in day t. It is known that $l(t)$ is a declining function of date within the spawning season (Dangel and Jones 1988; Perrin and Irvine 1990; Fukushima and Smoker 1997). Here, we use an exponential equation to express the stream life by date of entry:

$$(3) \qquad l(t) = \phi_1 e^{-\phi_2 (t-M)}$$

where ϕ_1 and ϕ_2 are two shape parameters estimated separately from independent stream life surveys and M is the mean date of arrival. The uncertainty in these two parameters is briefly considered in a sensitive analysis (see An application, Stream life estimates section below).

In our model, we assume that fish entering the stream on day ξ die $l(\xi)$ days later:

$$(4.1) \qquad \delta_{\xi+l(\xi)} = x_\xi = E e^{-(\xi-M)^2/(2S^2)} / \Psi$$

where $\delta_{\xi+l(\xi)}$ denotes the number of those fish that enter the stream in day ξ and die afterward on day $\xi + l(\xi)$. Due to the declining nature of our stream life function, it is possible that on some day, fish from several different entry days might die (this is not the case for a constant stream life where each entry day is mapped to a unique

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mortality day). We express the actual number of fish that died on day t as the sum over stream entry days:

$$(4.2) \quad d_t = \sum_{\{\xi\}} \delta_{\xi+l(\xi)} \quad \text{with } \xi \in \{\xi : \xi + l(\xi) = t\}$$

Thus, the spawning abundance can be expressed as

$$(5) \quad \eta_t = \sum_{k=1}^{t} x_k - \sum_{k=1}^{t} d_k$$

$$= \sum_{k=1}^{t} x_k - \sum_{k=1}^{t} \sum_{\{\xi\}} \delta_{\xi+l(\xi)}$$

$$= E\left(\sum_{k=1}^{t} e^{-(k-M)^2/(2S^2)} - \sum_{k=1}^{t} \sum_{\{\xi\}} e^{-(\xi-M)^2/(2S^2)} \right) / \Psi$$

$$= E\Phi_t$$

where

$$\Phi_t = \left(\sum_{k=1}^{t} e^{-(k-M)^2/(2S^2)} - \sum_{k=1}^{t} \sum_{\{\xi\}} e^{-(\xi-M)^2/(2S^2)} \right) / \Psi$$

the proportion of the total escapement alive in the stream on day t.

Let c_t denote the observed stream count on day t. We assume a normally distributed measurement error in the counts. Thus, we have

$$(6) \quad c_t = \eta_t + \varepsilon_t$$

where $\varepsilon_t \sim N(0,\sigma^2)$. Whenever necessary, the counts are transformed to meet the previous normal model assumptions (see A hierarchical methodology, The hierarchical model section below).

Separate estimation for each year

Given particular values of M, S, and E, the model equations above can be used to predict the number of fish in the stream on any date (η_t). Where we employed separate estimation below, maximum likelihood parameter estimates (MLEs) for a particular year were estimated using a nonlinear search algorithm that selected candidate values of M, S, and E to minimize SSQ, where SSQ was the following:

$$(7) \quad \text{SSQ} = \sum_{\{t\}} (c_t - \eta_t(M, S, E))^2$$

The estimate of σ^2 was calculated as SSQ/(no. of counts – no. of parameters).

Confidence intervals for each parameter were obtained by a bootstrap approach. In each bootstrap trial, residuals from the MLE fit were randomly sampled with replacement and added to the predicted counts to create a pseudo-data set. MLEs for these pseudo-data were then calculated. This bootstrap was repeated 3000 times (the percentiles became stable after about 500 iterations), and then the resulting estimates were ordered by size. Finally, the 2.5th and 97.5th percentiles were taken as the lower and upper bounds of the 95% confidence interval.

A hierarchical Bayesian methodology

The hierarchical model

Suppose that we have Y years of survey data for a stream. For year y, there are n_y counts. Let $c_{y,t}$ denote the observed count on survey day t for year y, M_y, S_y, and E_y the three unknown escapement parameters for year y, and σ^2 the data error variance. As in eq. 6, we have a model for the (possibly transformed) $c_{y,t}$ as

$$(8) \quad c_{y,t} | \theta_y, \sigma^2 \overset{\text{indep}}{\sim} N(\eta_{y,t}, \sigma^2), y = 1,\ldots,Y$$

where $\theta_y = (M_y, S_y, E_y)$. In this model, we allow for the possibility of a different timing and escapement in each year but assume a homogeneous measurement error for all years.

The hierarchical component of the model is the assumption that the timing of escapement is similar from year to year (Heard 1991). We express both the similarity and heterogeneity of escapement timing by assuming that the M_y and $\ln(S_y)$ are drawn from the following distributions:

$$(9) \quad M_y | \mu_m, \tau_m^2 \overset{\text{ind}}{\sim} N(\mu_m, \tau_m^2)$$

$$\ln(S_y) | \mu_s, \tau_s^2 \overset{\text{ind}}{\sim} N(\mu_s, \tau_s^2)$$

where μ_m and μ_s are population mean parameters and τ_m^2 and τ_s^2 are population variance parameters. Preliminary analysis of stream escapement data in our study area leads us to assume that M_y and $\ln(S_y)$ are independent of each other. Because of the high variability in abundance from year to year, we do not impose a hierarchical structure on the E_ys. Equations 8 and (or) 9 form a two-stage hierarchical model. There are in total $3Y + 5$ unknown parameters for this model, which are $\theta = (\{\theta_y\}, \sigma^2)$ (here, θ_y is redefined as the set $(M_y, \ln(S_y), E_y)$ and $y = 1,\ldots,Y$) and four hyperparameters $\lambda = (\mu_m, \tau_m^2, \mu_s, \tau_s^2)$.

For the purpose of simplicity, the error in counts is assumed to have the same variance (σ^2) for all years. However, annual escapements often fluctuate by many orders of magnitude. To achieve common measurement error variances, we could scale the observed counts for each year by dividing by the peak count $c_{y,p}$ (labeled "scaling"). This is equivalent to setting $\sigma_y = \sigma c_{y,p}$ but keeps our model in a simple form. Square root transformation (SQRT) (Quinn and Gates 1997) of the counts was also considered, and its performance was compared with scaling (we also explored a logarithm transformation (Hilborn et al. 1999)).

We denote the previous model the M_y–S_y model. Two more parsimonious models can be derived from the M_y–S_y model: (*i*) the M_y–S model with $\ln(S_y) = \ln(S)$ and parameters $\theta = (\{M_y, E_y\}, \ln(S), \sigma^2)$ and $\lambda = (\mu_m, \tau_m^2)$ and (*ii*) the M–S_y model with $M_y = M$ and parameters $\theta = (M, \{\ln(S_y), E_y\}, \sigma^2)$ and $\lambda = (\mu_s, \tau_m^2)$. We consider both the M_y–S and M–S_y models as alternatives, with scaling and SQRT as two data transformation options, but continue to focus on the more general M_y–S_y model in the narrative.

Prior specification

A full Bayesian analysis requires specifying prior distributions for the hyperparameters $\lambda = (\mu_m, \tau_m^2, \mu_s, \tau_s^2)$ and the data-level parameters $\{E_y\}$ and σ^2. We assume prior independence for all of these parameters. The prior specifications form the third stage of the HBM.

For μ_m and μ_s, we set their priors as $\mu_m \sim N(a_m, V_m)$ and $\mu_s \sim N(a_s, V_s)$, where a_m, V_m, a_s, and V_s are constants to be specified by the modelers. Choosing large V_m and V_s will make these two prior distributions relatively uninformative but still proper (Spiegelhalter et al. 1997) (a proper prior is a prior density, say, $p(\vartheta)$, that can integrate to 1 (or any positive finite value), i.e., the integral $\int p(\vartheta | y) d\vartheta$ is a constant).

The specification of the priors of the population variance parameters (e.g., τ_m^2 and τ_s^2) needs special treatment in a HBM because an automatic use of the standard "uninformative" improper priors (e.g., $p(\sigma^2) \propto 1/\sigma^2$) for these parameters might lead to improper posteriors (Gelman et al. 1995; Hobert and Casella 1996) (for an improper posterior density, say $p(\vartheta|y)$, the integral $\int p(\vartheta|y) d\vartheta$ is not finite for all y). The safest way to get around this problem is by specifying proper prior distributions for these parameters. We set the priors for τ_m^2 and τ_s^2 as inverse gamma distributions (IG) (see Gelman et al. 1995): $\tau_m^2 \sim \text{IG}(c_m, d_m)$ and $\tau_s^2 \sim \text{IG}(c_s, d_s)$, respectively. To obtain uninformative priors for these hypervariance pa-

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rameters, we set $c = d = \varepsilon$, where ε is a small positive value (Spiegelhalter et al. 1997).

For convenience, uninformative priors are specified for the remaining parameters: $E_y \sim U(0,\infty)$ and $\sigma^2 \sim \text{IG}(0.001,0.001)$. Similar priors are specified for the M_y–S and M–S_y models.

Combining the priors, population distributions, and likelihood (see Hilborn et al. 1999), we obtain the joint posterior distribution for all the parameters in the M_y–S_y model as

$$(10)\quad p(\theta,\lambda\,|\,D) \propto p(\lambda)p(\sigma^2)\prod_{y=1}^{Y} N(M_y\,|\,\mu_m,\tau_m^2) \times \prod_{y=1}^{Y} N(\ln(S_y)\,|\,\mu_s,\tau_s^2)\prod_{y=1}^{Y} p(E_y)\prod_{t=1}^{n_y} N(c_{y,t}\,|\,\eta_{y,t},\sigma^2)$$

where $p(\lambda) = p(\mu_m)\,p(\tau_m^2)\,p(\mu_s)\,p(\tau_s^2)$ and D denotes observed data.

For the M_y–S model, we have

$$(11)\quad p(\theta,\lambda\,|\,D) \propto p(\lambda)\;p(\ln(S))p(\sigma^2) \times \prod_{y=1}^{Y} N(M_y\,|\,\mu_m,\tau_m^2)\prod_{y=1}^{Y} p(E_y)\prod_{t=1}^{n_y} N(c_{y,t}\,|\,\eta_{y,t},\sigma^2)$$

where $p(\lambda) = p(\mu_m)p(\tau_m^2)$.

For the M–S_y model, the joint posterior distribution is

$$(12)\quad p(\theta,\lambda|\,D) \propto p(\lambda)p(M)p(\sigma^2) \times \prod_{y=1}^{Y} N(\ln(S_y)\,|\,\mu_s,\tau_s^2)\prod_{y=1}^{Y} p(E_y)\prod_{t=1}^{n_y} N(c_{y,t}\,|\,\eta_{y,t},\sigma^2)$$

Where $p(\lambda) = p(\mu_s)p(\tau_s^2)$.

MCMC: an adaptive hybrid Metropolis–Gibbs sampler

We choose a hybrid MCMC algorithm, the Metropolis–Gibbs sampler (Tierney 1994), to evaluate our complex joint posterior distributions. The hierarchical model structure and our specification of appropriate conjugate priors enabled us to derive full conditional distributions with familiar distributional forms (e.g., normals and inverse gammas) for most of the parameters in our HBM. This allowed use of Gibbs sampling (Geman and Geman 1984; Gelfand and Smith 1990), a means of generating sample values from the joint posterior distribution by sequential draws from the full conditional distributions. Nonstandard forms for the distribution of the escapement timing parameters required embedding Metropolis steps within the Gibbs procedure (Tierney 1994; Carlin and Louis 1996).

The Gibbs sampler and the full conditional distributions

The Gibbs sampler generates random draws for all the parameters by sampling successively from the full posterior conditional distribution of each parameter $p(\varphi_i|\{\varphi_j\}_{j\neq i},D)$, $i = 1,\ldots, p$, where $\{\varphi_j\}_{j\neq i}$ is the set of all of the parameters of a model except for φ_i. Under very broad conditions (Geman and Geman 1984), the Gibbs sampler produces a Markov chain with the joint posterior distribution as its equilibrium distribution. Consequently, the sampled values of φ_i from the Gibbs sampler after convergence can be regarded as random draws obtained from its marginal posterior distribution. Thus, simple summary statistics and kernel density estimates based on these draws can be used to summarize the marginal posterior distribution for each parameter.

The full conditional distribution of a parameter is obtained by extracting the terms in the posterior distribution only involving that parameter (its prior and likelihood) and treating all other terms as constants. For example, the terms involving μ_m in eq. 10 are its prior term $p(\mu_m) = N(\mu_m|a_m,V_m)$ and its likelihood term.

$$\prod_{y=1}^{Y} N(M_y|\mu_m,\tau_m^2)$$

The likelihood term, treated as a function of μ_m, can be shown to be $N(\mu_m|\hat{\mu}_m,\tau_m^2/Y)$, where

$$\hat{\mu}_m = \left(\frac{1}{Y}\right)\sum_{y=1}^{Y} M_y$$

Multiplying the likelihood by the prior, we obtain

$$(13)\quad \mu_m|\{M_y\},\tau_m^2 \sim N\left[\frac{a_m\tau_m^2 + Y\hat{\mu}_m V_m}{\tau_m^2 + YV_m},\frac{V_m\tau_m^2}{\tau_m^2 + YV_m}\right]$$

Similarly, we derived the rest of the full conditionals for the M_y–S_y, M_y–S and M–S_y models, and these are listed as follows:

$$(14)\quad \tau_m^2|\{M_y\},\mu_m \sim \text{IG}(c_m + Y/2, d_m + Y\hat{\tau}_m^2/2)$$

where

$$\hat{\tau}_m^2 = \frac{1}{Y}\sum_{y=1}^{Y}(M_y - \mu_m)^2$$

$$(15)\quad \mu_s|\{\ln(S_y)\},\tau_s^2 \sim N\left[\frac{a_s\tau_s^2 + Y\hat{\mu}_s V_s}{\tau_s^2 + YV_s},\frac{V_s\tau_s^2}{\tau_s^2 + YV_s}\right]$$

with

$$\hat{\mu}_s = \frac{1}{Y}\sum_{y=1}^{Y}\ln(S_y)$$

$$(16)\quad \tau_s^2|\{\ln(S_y)\},\mu_s \sim \text{IG}(c_s + Y/2, d_s + Y\hat{\tau}_s^2/2)$$

where

$$\hat{\tau}_s^2 = \frac{1}{Y}\sum_{y=1}^{Y}(\ln(S_y) - \mu_s)^2$$

$$(17)\quad \sigma^2|\{M_y,\ln(S_y),E_y\} \sim \text{IG}(c_1 + n/2, d_1 + n\hat{\sigma}^2/2)$$

where

$$\hat{\sigma}_2 = \frac{1}{n}\sum_{y=1}^{Y}\sum_{t=1}^{n_y}(c_{y,t} - \eta_{y,t})^2$$

and

$$n = \sum_{y=1}^{Y} n_y$$

$$(18)\quad E_y|M_y,\ln(S_y),\sigma^2 \sim N(\hat{\mu}_{E_y},V_{E_y})$$

where

$$\hat{\mu}_{E_y} = \sum_{t=1}^{n_y}(\Phi_{y,t}c_{y,t})\Big/\sum_{t=1}^{n_y}(\Phi_{y,t})^2$$

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$$V_{E_y} = \sigma^2 \Big/ \sum_{t=1}^{n_y} (\Phi_{y,t})^2$$

(19) $$p(M_y|\mu_m, \tau_m^2, \ln(S_y), E_y, \sigma^2) \propto N(\mu_m, \tau_m^2) \exp\left(-\frac{1}{2\sigma^2} \sum_{t=1}^{n_y} (c_{y,t} - \eta_{y,t})^2 \right)$$

(20) $$p(\ln(S_y)|\mu_s, \tau_s^2, M_y, E_y, \sigma^2) \propto N(\mu_s, \tau_s^2) \exp\left(-\frac{1}{2\sigma^2} \sum_{t=1}^{n_y} (c_{y,t} - \eta_{y,t})^2 \right)$$

For the M_y–S model, eqs. 15, 16, and 20 are replaced by

(21) $$p(\ln(S)|\{M_y, E_y\}, \sigma^2 \propto N(\ln(S)|a_s, V_s) \exp\left(-\frac{1}{2\sigma^2} \sum_{y=1}^{Y} \sum_{t=1}^{n_y} (c_{y,t} - \eta_{y,t})^2 \right)$$

For the M–S_y model, eqs. 13, 14, and 19 are replaced by

(22) $$p(M|\{\ln(S_y), E_y\}, \sigma^2) \propto N(M|a_m, V_m) \exp\left(-\frac{1}{2\sigma^2} \sum_{y=1}^{Y} \sum_{t=1}^{n_y} (c_{y,t} - \eta_{y,t})^2 \right)$$

The Metropolis steps

The full conditional distributions for the parameters M_y, $\ln(S_y)$, $\ln(S)$, and M (eqs. 19–22) are not in closed form due to the nonlinearity of the spawning abundance model. It is not straightforward to generate random values from these distributions. We apply Metropolis steps to sample from each of these conditionals (Carlin and Louis 1996). For more details of the implementation of Metropolis steps, see Appendix A.

In Appendices B and C, we also provide further details for the implementation of the MCMC convergence diagnostics and model comparison and adequacy checking.

An application

Kadashan Creek pink salmon

We applied the HBM to estimate historical pink salmon escapements for Kadashan Creek in Southeast Alaska. Escapement counts for this stream were obtained from the Alaska Department of Fish and Game Integrated Database (Van Alen 2000). Most of these counts are collected through aerial escapement surveys.

In this paper, we illustrate the results for Kadashan Creek over the period 1974–1998. Escapement counts from this stream vary considerably among years in both frequency and duration (Fig. 1). The scale of the counts also varies by severalfold across years, necessitating transformation of the counts. However, scatter plots of the counts suggest similar run timing among years. Thus, the hierarchical approach seems reasonable for this stock.

Stream life estimates

The relationship between stream life and entry date was estimated outside of the HBM framework. Dangel and Jones (1988) studied stream life of pink salmon spawners in several streams in Southeast Alaska: the Kadashan River in 1986 and Pleasant Bay Creek, Black Bear Creek, and Sashin Creek in 1986 and 1987. We used these data to estimate the decline in stream life with date as follows. First, we centered the stream life values for each stream in each year around the mean date of the corresponding stream entry (obtained from the weir data of Dangel and Jones 1988). We then combined the data from all streams (Fig. 2) and fitted them to the stream life equation, eq. 3. The estimated parameter values were $\hat{\phi}_1 = 14.16$ and $\hat{\phi}_2 = 0.0284$.

The period when Kadashan Creek was surveyed in 1986 was from July 31 to August 10, much shorter than the period of the stream entry (July 18 to August 28). Nevertheless, we fit eq. 3 to the Kadashan data and obtained $\hat{\phi}_1 = 11.8$ and $\hat{\phi}_2 = 0.0078$ (a small declining rate) for this creek. These parameters imply that stream life in Kadashan Creek was approximately constant. We looked at the effect of assuming a constant stream life (set to 11.8 ($\hat{\phi}_1$)) and compared the results using this assumption (referred to as CnSL) with those obtained assuming a declining stream life.

Details of estimation

We estimated escapement, the date of peak escapement, and the standard deviation in date of escapements for historical Kadashan Creek data using the M_y–S_y, M_y–S, and M–S_y models and separate estimation of each year. A Pascal program running under the Borland Delphi environment was developed to perform all the calculations. We used both the scaling and SQRT transformations of count data from 1974 to 1998. Because of convergence problems, some model comparisons were made using only data from 1977 to 1998 (see Results below).

The data appeared to contain ample information to estimate μ_m, μ_s, the E_ys, and σ^2 (see Results below). We specified uninformative priors for these parameters: $\mu_m \sim N(210, 10^5)$, $\mu_s \sim N(2.5, 10^3)$, $E_y \sim U(0,\infty)$, and $\sigma^2 \sim \text{IG}(0.001, 0.001)$.

We set $\tau_m^2 \sim \text{IG}(0.001,0.001)$. The data seemed less informative for the population variance parameters τ_m^2 and τ_s^2 in the M_y–S_y model, especially for the latter (see Results below). Accordingly, we checked the sensitivity of the posterior estimates to the specification of the prior of τ_s^2. Under the scaling transformation, we compared the priors IG(0.01,0.01) and IG(0.1,0.1). Under the SQRT transformation, we compared the priors IG(0.001,0.001) and IG(0.01,0.01).

For the M_y–S model, we set $p(\ln(S)) \propto N(2.5,10^3)$. For the M–S_y model, we set $p(M) \propto N(210,10^5)$ and $\tau_s^2 \sim \text{IG}(0.001,0.001)$. Other priors were kept the same as for the M_y–S_y model.

Results

Convergence diagnostics

We first describe in detail the steps taken to assess convergence (Appendix B) for the M_y–S_y model with the scaling transformation of the counts. Similar processes were repeated for other models and data transformations.

The MCMC did not converge if we used the M_y–S_y model with the complete data set. A fundamental ambiguity existed between τ_m^2 and τ_s^2. The MCMC would spend long periods with either τ_m^2 or τ_s^2 at a value of zero, effectively reducing the M_y–S_y model to one of its simpler forms. Using these simpler forms, the M_y–S and M–S_y models, the MCMC did converge. The M_y–S_y also converged when the first three years of the data series, which were very uninformative, were discarded.

We ran the Gibbs sampler an initial 3000 iterations to tune the standard deviations of the proposal distributions used in the Metropolis steps to draw values of M_y and S_y so as to obtain an acceptance rate in the range of 40–60% for each of these parameters (Appendix A). We then ran the Gibbs sampler for an additional 5000 iterations. The results from these 5000 iterations showed that the hyperparameters and the

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Fig. 1. Count data (circles) and model fits for Kadashan Creek, 1974–1998. The solid line is the fit of the M_y–S model using scaled counts and a nonconstant stream life. The broken line is the fit obtained by separate estimation of each year.

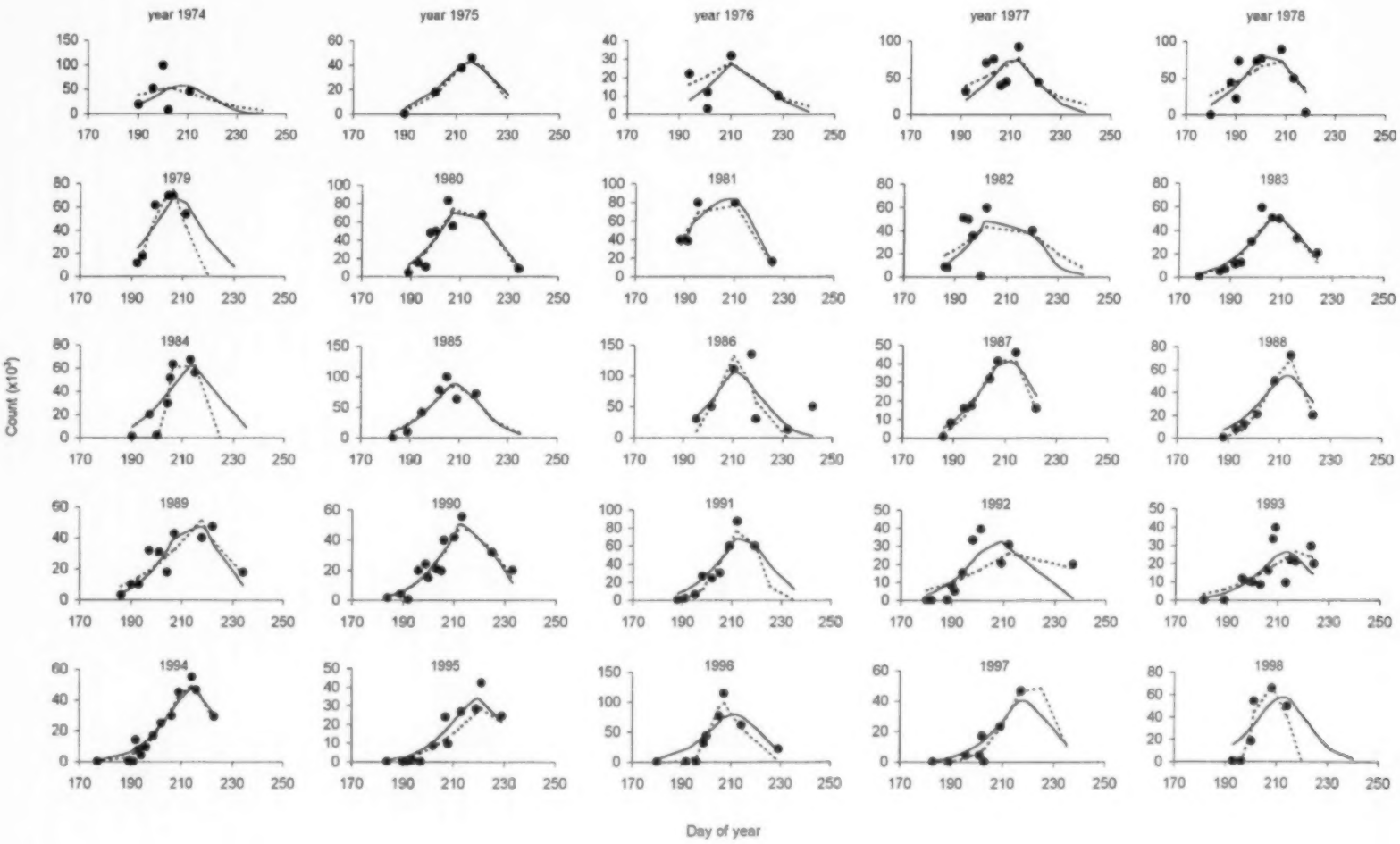

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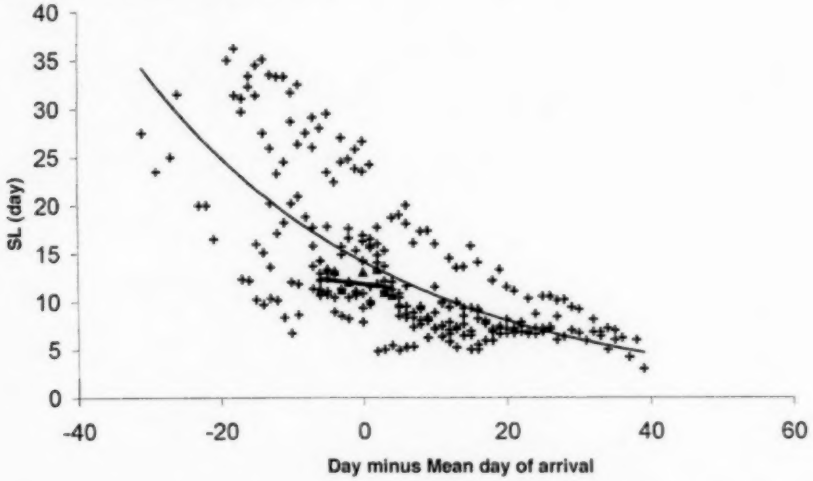
Fig. 2. Combined stream life (SL) data and those for Kadashan Creek from Dangel and Jones (1988) and the exponential fitting curves for these two data sets. Crosses denote combined SL data and triangles denote SL data for Kadashan Creek. The thin line is the fit for combined data and the heavy line is for the Kadashan data.



timing parameters had relatively high autocorrelations (lag 1 autocorrelations range from 0.8 to 0.9). Their autocorrelation function decayed slowly, approaching zero only after about lag 15. In contrast, most of the escapement parameters had low autocorrelations. The Raftery and Lewis (1992) convergence diagnostic (Appendix B) indicated that τ_m^2 and τ_s^2 were the slowest to converge, requiring 35 000 iterations in order to get an accuracy for the 2.5th percentiles within ±0.005 with 95.5% probability.

Due to these autocorrelations, we reran the Gibbs sampler for 200 000 iterations with a thinning interval of 20. This time, all diagnostics were satisfied. We then ran another Gibbs sampler sequence with different starting values, and Gelman and Rubin's (1992) diagnostic (Appendix B) indicated convergence of the chains. Thus, the output after convergence was used for subsequent inference.

Model checking and comparison

Table 1 shows the values of the coefficients of skewness and kurtosis of the standardized residuals (Appendix C). The value of skewness for all cases is near zero, indicating that the standardized residuals achieve reasonable symmetry in their distributions (Snedecor and Cochran 1982) and implying that the models are neither overfitted nor underfitted. The values of the kurtosis indicate possible heavy tails in the distribution, less so with the scaling than the SQRT transformation. We also explored a logarithmic data transformation (not shown) and found it to be worse than SQRT. In summary, scaling the counts seems slightly more appropriate for this data set than SQRT.

Table 1 also reports the values of model comparison quantities (Appendix C). With scaling, the M_y–S model has the smallest value of the negative cross-validation log-likelihood (ncvLogL) (Appendix C), indicating that it is preferred. The values of the deviance information criterion (DIC) for the M_y–S_y and M_y–S models are very close, so the M_y–S model would also be the preferred model according to the principle of parsimony. The values of both ncvLogL and DIC indicate that the M–S_y model fit the data less well than the other two models. Under SQRT, the two model comparison criteria favor the M_y–S_y model more than the simpler models. Under both data transformations, the estimated effective number of parameters (p_D) for the M_y–S_y model is in the range of 43–47 versus the nominal value of 71. For the two simpler models, the values of p_D are in the range of 38–41 versus the nominal value of 48.

Sensitivity to the prior

Preliminary analyses indicated that τ_s^2 was the parameter most sensitive to prior specifications with the M_y–S_y model. Under scaling, with two priors of τ_s^2 (IG(0.01,0.01) and IG(0.1,0.1)), the posterior medians and 95% credible intervals of τ_s^2 were 0.023 (0.004, 0.127) and 0.069 (0.024, 0.244), respectively (see the values in the bordered area in Table 2). The first prior has a peak at 0.0099 and the latter at 0.09, indicating that the priors tended to pull the posteriors towards their modes. Under SQRT transformation, the posteriors of τ_s^2 were not so sensitive, but their left tails seemed to be influenced by the priors. The other parameters were much more robust to their priors, especially the population means and the yearly parameters (Table 2).

Data transformations, model forms, and posterior estimates

For the M_y–S_y and M_y–S models, posterior inference was more similar under the same data transformation than between the data transformations (Table 2). The M–S_y model obtains slightly different results compared with other two models. When using the simpler models that fix aspects of escapement timing, more variation is attributed to the remaining set of timing parameters and the measurement error (see the increased values of τ_m^2, τ_s^2, and (or) σ^2 compared with those of the M_y–S_y model (Table 2)).

The 95% credible intervals of E_y were the most sensitive to the data transformation (Table 2). Scaling produced narrower 95% credible intervals of E_y than SQRT for most

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Table 1. Model checking and choice quantities for data from 1977 to 1998.

Measurement	Coefficient of skewness	Kurtosis	ncvLogL	$\bar{D}$	p_D	DIC
Scaling						
M_y–S_y[a]	0.138	4.16	–6.3	–86.8	42.8	–43.9
M_y–S_y[b]	0.108	4.16	–5.3	–87.7	44.6	–43.1
M_y–S	0.181	4.13	–7.3	–84.2	40.9	–43.3
M–S_y	0.259	3.31	3.8	–48.3	39.2	–9.1
SQRT						
M_y–S_y[c]	–0.385	4.73	1073.5	2076.4	47.0	2123.4
M_y–S_y[d]	–0.385	4.74	1073.0	2078.6	45.2	2123.8
M_y–S	–0.189	5.76	1074.6	2097.4	38.2	2135.6
M–S_y	–0.307	4.20	1078.3	2106.2	41.0	2147.2

Note: ncvLogL= $-\Sigma\log(\text{cpo}_y)$, the negative cross-validation log-likehood, $\bar{D}$ is the posterior mean of deviance, p_D is the effective number of parameters, and DIC is the deviance information criterion (Appendix C).

[a]Prior for $\tau_s^2 \sim$ IG(0.01,0.01).

[b]Prior for $\tau_s^2 \sim$ IG(0.1,0.1).

[c]Prior for $\tau_s^2 \sim$ IG(0.001,0.001).

[d]Prior for $\tau_s^2 \sim$ IG(0.01,0.01).

years. The SQRT transformation has the property of down-weighting the large counts and up-weighting the small counts. Thus, the tail area of the count curves was fit better than with scaling, but fits around the peaks could be quite different. For the years 1979, 1984, 1991, and 1998, which are years with a single count shortly after the observed peak, SQRT would quite often treat this count as a value with large observation error rather than a point containing important information about escapement timing. This may be the reason that SQRT produced large variance estimates of escapements for these years.

The M–S_y model yields narrower 95% credible intervals of E_y than the other two models, especially under SQRT (see bolded values in Table 2). By forcing the M_y to a common value, we greatly reduce the uncertainty in E_y for years with little postpeak data (Figs. 1 and 3).

The posterior distributions of M_y and E_y achieve reasonable symmetry for the informative years (e.g., 1980, 1983, 1989, and 1990, etc.) under both kinds of data transformations (Fig. 4). However, posterior distributions of M_y and E_y are positively skewed for years such as 1974, 1975, 1979, 1984, 1991, 1992, 1997, and 1998 (Fig. 4), which are years with few or no postpeak counts (Fig. 1).

Effects of stream life

Assumptions about stream life appeared to be very important in determining the magnitude of the escapement estimates and also influenced estimates of variance. Using a constant stream life resulted in posterior medians of the E_y that were bigger and 95% credible intervals that were wider than with a nonconstant stream life (see bolded values in the bordered area in Table 2). We separately analyzed the effects of the two parameters of our stream life model (eq. 3). For a fixed ϕ_2, the three yearly parameters increase as ϕ_1 decreases. When ϕ_1 is fixed, M_y and S_y decrease and E_y increases as ϕ_2 decreases.

Comparison of the HBM with separate estimation of each year

Table 3 compares the posterior estimates obtained from the M_y–S_y model with scaling with the bootstrap estimates from separate estimation for four representative years. The 1990 data (Fig. 1) contain two postpeak counts, one many days past the peak, and the counts show no apparent pulses. The 1992 data contain three postpeak counts but have apparent pulses and one possible outlier that result in a large amount of "measurement" error. The 1997 data have no postpeak counts, while the 1998 data have one count shortly after the peak.

In all cases, separate estimates match the observed count data more closely than the HBM fit but differ more among years in run timing (Fig. 1). Nevertheless, the quality of the separate estimates is more sensitive to that of the data (Table 3). Where the data are informative (e.g., 1990), the point estimates (medians) from these two approaches are comparable (Table 3); confidence intervals using the HBM are wider because the HBM approach considers the properties of other years where counts suggest different run timing. In years where no postpeak counts exist (e.g., 1997) or the data have irregular features (e.g., 1992, 1998 (with an anomalous run timing)), separate estimation is unable to unambiguously determine the run timing (see bolded medians and confidence intervals in Table 3) and consequently the escapement, whereas HBM is able to use the shapes of other years' timing curves to narrow the uncertainty considerably.

Simulation studies (Adkison and Su 2001, table 4) show that the bootstrap confidence intervals from separate estimation underestimate the uncertainty of the parameters, while the HBM provides approximately correct uncertainty estimates. This may explain some of the instances of seemingly more precise estimates for separate estimation.

Discussion

In this paper, we have extended escapement estimation methods such as the deterministic area-under-the-curve method (English et al. 1992) and statistical modeling of each year separately (Quinn and Gates 1997; Hilborn et al. 1999) to a hierarchical Bayesian paradigm. Methods that treat each year's data separately are prone to failure in years where count data are sparse, particularly if counts are lacking after the peak in escapement (Hilborn et al. 1999; Adkison and Su 2001). Our HBM approach is able to use historical escapement data for a stream to "borrow strength" from years with good data to obtain improved annual estimates for escapement and its timing in years with poor data.

Our approach also differs from traditional escapement estimation methods in incorporating the well-known decline in longevity on the spawning grounds as the season progresses (Perrin and Irvine 1990). The Kadashan example shows that spawning abundance models are sensitive to assumptions about stream life, in particular in estimating the magnitude of escapement. Since stream life can vary by year as well as by date within a year, this is an important source of error in escapement estimation.

Observer efficiency can be another important factor influencing escapement estimation. It is known that aerial and foot surveys often undercount the number of spawners pre-

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Table 2. Posterior summary for the hyperparameters and annual parameters obtained from the M_y–S_y, M_y–S, and M–S_y models under two types of data transformation and two stream life models using data from 1977 to 1998.

Data transformation		μ_m (M)	τ_m^2	μ_s (ln(S))	τ_s^2	σ^2	M_y	ln(S_y)	E_y ($\times 10^3$)
Scaling	M_y–S_y[a]	207.7	20.1	2.6	0.023	0.038	207.6	2.6	110.5
		(205.0, 210.9)	(7.5, 48.7)	(2.4, 2.8)	(0.004, 0.127)	(0.03, 0.05)	(10.5)	(0.7)	(68.6)
	M_y–S_y[b]	207.8	18.6	2.6	0.069	0.038	207.7	2.6	110.1
		(205.1, 211.1)	(5.5, 47.0)	(2.4, 2.9)	(0.024, 0.224)	(0.03, 0.05)	(11.3)	(0.9)	(69.4)
	M_y–S	207.7	21.7	2.6		0.038	207.6		111.4
		(205.2, 210.8)	(10.0, 51.4)	(2.4, 2.8)		(0.03, 0.04)	(9.4)		(68.0)
	M–S_y	209.6		2.8	0.096	0.046		2.8	113.3
		(207.7, 212.2)		(2.5, 3.0)	(0.028, 0.268)	(0.04, 0.06)		(0.8)	**(66.6)**
	M_y–S_y[c] (CnSL)	206.5	22.5	2.4	0.029	0.035	206.4	2.4	**142.8**
		(204.1, 209.2)	(10.3, 52.8)	(2.2, 2.5)	(0.005, 0.128)	(0.03, 0.05)	(9.3)	(0.7)	**(102.3)**
SQRT	M_y–S_y[d]	208.3	21.6	2.5	0.049	2123	208.2	2.5	108.6
		(205.7, 211.5)	(6.3, 53.6)	(2.3, 2.7)	(0.002, 0.216)	(1680, 2725)	(11.9)	(0.8)	(105.1)
	M_y–S_y[e]	208.4	21.0	2.5	0.063	2097	208.2	2.5	108.4
		(205.7, 211.5)	(6.3, 54.2)	(2.3, 2.7)	(0.010, 0.236)	(1653, 2706)	(11.9)	(0.8)	(103.1)
	M_y–S	208.4	22.6	2.5		2328	208.4		108.9
		(205.7, 211.7)	(9.2, 57.1)	(2.4, 2.6)		(1874, 2947)	(10.8)		(111.0)
	M–S_y	209.2		2.6	0.122	2434		2.6	108.4
		(207.5, 211.2)		(2.4, 2.8)	(0.044, 0.325)	(1964, 3089)		(0.8)	**(88.3)**

Note: For the hyperparameters and σ^2, the median of the posterior distribution is shown with the boundaries of the 95% credible interval below in parentheses. For the annual parameters, the average across years of the posterior median is given with the average width of the 95% credible interval below in parentheses.

[a]Prior for $\tau_s^2 \sim$ IG(0.01,0.01).

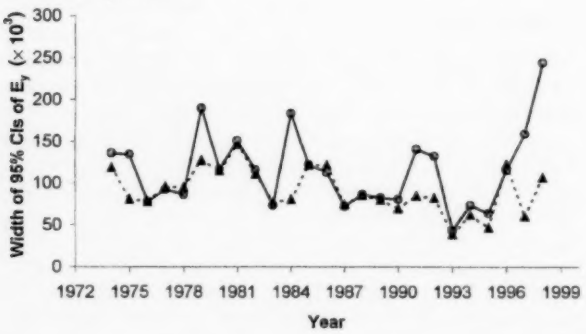
[b]Prior for $\tau_s^2 \sim$ IG(0.1,0.1).

[c]Assumes that stream life is a constant (CnSL) rather than declining with date.

[d]Prior for $\tau_s^2 \sim$ IG(0.001,0.001).

[e]Prior for $\tau_s^2 \sim$ IG(0.01,0.01).

Fig. 3. Width of the 95% credible interval (CI) for E_y for each year. Results are shown for the M_y–S and M–S_y models using the SQRT transformation of the counts and a nonconstant stream life. The solid line is for the M_y–S model and the dashed line is for the M–S_y model.



sented in a stream, especially when the density of the fish is high (Jones et al. 1998). Within- and between-observer variability and bias of counts are also observed (Jones et al. 1998). The pink salmon counts that we used here have been partially corrected for bias (Van Alen 2000). Hilborn et al. (1999) suggested that weir studies on index streams should be used to estimate observer bias and stream life.

In our example, we found that appropriate error assumptions for the counts and simplification of the HBM were necessary for convergence of the Gibbs sampler. For example, the Gibbs sampler may fail to converge under the M_y–S_y model setting if the counts are not transformed because the scale of the counts for different years may vary by several orders of magnitude. The scaling and SQRT transformations proposed here are both able to address this problem, but the scaling transformation seemed to work better in our example. Nevertheless, the difference between SQRT and scaling fits in these sorts of cases was smaller than that resulting from using a separate estimation approach, where data from uninformative years did not constrain escapement timing.

Further refinement of the HBM is possible. Pulsed entry (caused by irregular fishing and variability in the entry process) is typical for salmon escaping to spawning streams. Although these pulses are smoothed by the overlap of spawners who have entered the stream on different days, spikes in counts are still quite visible in much stream data. This kind of variation (caused by the variability in entry process) is not counted in the spawning abundance model explicitly but is treated as observation error. Excessive "observation" error in combination with few postpeak counts can cause convergence problems for the Gibbs sampler.

In our example, we were unable to differentiate variability in the mean date of escapement (τ_m^2) from variability in the duration of escapement (τ_s^2). By retreating to the simpler M_y–S or M–S_y model, we were able to complete the analysis. Refined stream entry models that used environmental conditions, such as floods and rainfall, might explain some of the higher-frequency variation in spawner counts and thus increase the estimability of the timing parameters of the HBM.

As Millar and Meyer (2000) pointed out, "Fitting a model is just the beginning." In this paper, we addressed the important problem of model selection and adequacy using predic-

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Fig. 4. Posterior median and 95% credible interval for (*a*) M_y and (*b*) E_y for each year. Results are shown for the M_y–S model using scaled counts and a nonconstant stream life.

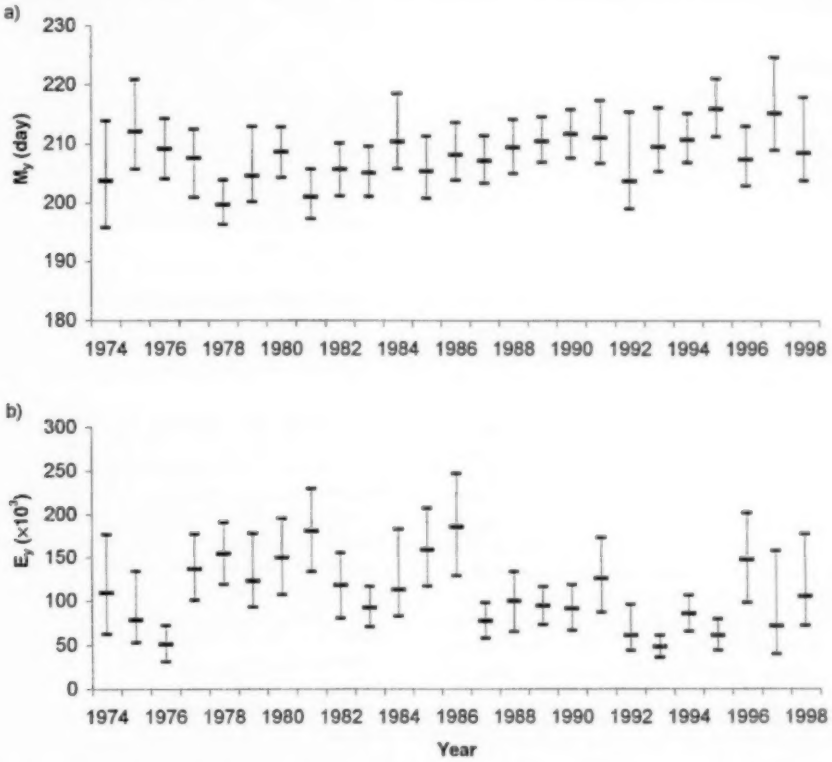

Table 3. Posterior summary (median with the 95% credible interval below in parentheses) for the annual parameters obtained from an HBM (the M_y–S_y model with scaling with priors for $\tau_m^2 \sim$ IG(0.001,0.001) and for $\tau_s^2 \sim$ IG(0.01,0.01)) versus the bootstrap summary statistics (median with the 95% confidence interval below in parentheses) from separate estimation (SepEst) for four divergent years (see text).

	M_y		S_y		E_y ($\times 10^3$)	
Year	HBM	SepEst	HBM	SepEst	HBM	SepEst
1990	211.3	212.8	13.4	14.7	90.7	97.6
	(207.4, 215.4)	(210.1, 216.6)	(9.9, 18.4)	(11.2, 19.8)	(66.6, 116.1)	(83.9, 111.9)
1992	203.4	226.4	13.9	**35.1**	59.8	76.9
	(198.2, 215.7)	(203.8, **>350.0**[a])	(9.3, 21.0)	(14.4, **>100.0**[b])	(35.9, 93.1)	(37.4, **209.9**)
1997	214.1	216.4	12.1	10.7	68.8	**86.5**
	(208.2, 222.8)	(207.9, **>350.0**[a])	(7.8, 16.6)	(4.2, 40.1)	(39.7, 142.4)	(43.2, **1.9 × 10^6**)
1998	207.9	200.8	12.8	**1.0**	97.7	**66.6**
	(202.7, 215.9)	(**200.7, 200.8**)	(8.3, 18.0)	(**<1.0**[c], **1.9**)	(69.6, 152.1)	(60.7, **71.0**)

[a]The value 350.0 is the upper bound of the constraint set for M_y.
[b]The value 100.0 is the upper bound of the constraint set for S_y.
[c]The value 1.0 is the lower bound of the constraint set for S_y.

tive model determination techniques. Such validation steps are rare in fisheries applications of Bayesian methods, probably due to the computational burden. Bayesian methods require much effort just for model fitting; sometimes, model assessment and selection are not well addressed (Millar and Meyer 2000). The Gibbs sampler and other MCMC techniques enable users to tackle complex models those are impossible to cope with by other methods. The predictive model determination quantities that we used in this example can be easily calculated in the Gibbs sampling process, so routine model checking should not be too onerous.

An additional method of borrowing strength would be to incorporate spatial relationships as another hierarchical level in the model. In Southeast Alaska, pink salmon in neighboring streams often have similar run timing. They also experience correlated fluctuations in escapement, in response to both a common environment and a common harvest regime. Incorporating these common patterns would reduce the un-

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certainty in escapement estimates even further. Weir studies on representative index streams would further increase the benefit of this approach.

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Appendix A. The Metropolis steps

We use a Metropolis step with a normal proposal distribution $N(\vartheta_i^* | \vartheta_i^{(t-1)}, \mathrm{SD}_i^2)$, $i = 1,\ldots,p$, to update each of those parameters with no standard-form full conditional distributions, where $\vartheta_i^{(t-1)}$ is the current value of a parameter, ϑ_i^* is a candidate value, and SD_i is a specified standard deviation for the proposal distribution. In a Metropolis step, ϑ_i^* is accepted as an update with probability $\min(1, p(\vartheta_i^* | \{\vartheta\}_{j \neq i}) / p(\vartheta_i^{(t-1)} | \{\vartheta\}_{j \neq i}))$; otherwise, it is rejected and we set $\vartheta_i^{(t)} = \vartheta_i^{(t-1)}$.

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The choice of SD_j affects the efficiency of Metropolis steps and thus the whole algorithm. High values of SD_j result in large proposal moves and low acceptance rate because most of the candidate moves may step into low-density areas of the posterior distribution and thus be rejected. Small values of SD_j result in high acceptance rate and slow movement of the chain.

The performance of the Metropolis algorithm can be expressed by the acceptance rate of the candidate draws in the Metropolis steps. Theoretical and empirical results show that the acceptance rate in the range of 20–50% (depending on the number of parameters) provides optimal performance (Gelman et al. 1995). For multilevel models, Browne and Draper (2000) proposed an acceptance rate of 40–60% for univariate updating.

To increase the efficiency of the Metropolis algorithm, we adopt an adaptive tuning step similar to that of Browne and Draper (2000) to tune the SD_j before generating sample draws for inference. The goal of the tuning is to obtain a target acceptance rate of around 50%. The adaptive step is stopped after a fixed number of iterations, after which the burn-in period (the preconvergence period) and main monitoring run (the postconvergence period) are started.

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Appendix B. Markov chain Monte Carlo convergence diagnostics

A critical issue in using MCMC methods is how to determine when random draws have converged to the posterior distribution (Gelman et al. 1995). Best et al. (1995) have developed a collection of S-plus routines called CODA for convergence diagnostics of MCMC sampling. Several general diagnostic methods have been incorporated in this free package, including methods proposed by Geweke (1992), Heidelberger and Welch (1983), Raftery and Lewis (1992), and Gelman and Rubin (1992). CODA also provides summary estimates, kernel density plots, autocorrelations, and cross-correlations for the monitored quantities. We used the results from these CODA routines to assess convergence of our MCMCs. We provide a summary of their underlining theoretical considerations, implementation, and criteria for assessing convergence in Table B1.

Table B1.

Aspect monitored	Diagnostic	No. of chains	Diagnostic steps	Theory and convergence criteria
Trend	Geweke 1992	Single	(1) Compare the mean in the first x% (e.g., 10%) portion of the simulation output of a quantity of interest with that containing the last y% (e.g., 50%) of the output by a Z score (2) If $\|Z\|$ is extreme, the first x% can be discarded and the Geweke diagnostic be repeated and so on	If the chain is in stationary, the means of the values early and late in the sequence should be similar. The diagnostic is a Z score that is the difference of the two means divided by an asymptotic standard error of the difference of the means. As length of chain $\rightarrow \infty$, $Z \rightarrow N(0,1)$, so Geweke $\|Z\| < 2$ means convergence
	Heidelberger and Welch 1983	Single	(1) Conduct a test for the null hypothesis of stationarity for the entire simulation output of a quantity first (2) If the null hypothesis is rejected, the test is repeated after discarding the first, e.g., 10% of the series. This process will continue until either the null hypothesis is passed or 50% of the iterations have been discarded and the null hypothesis is still rejected. In the latter case, CODA will report the failure of the stationarity test and the value of the Cramer – von Mises (C-vonM) statistic	Use a Brownian bridge theory and the C-vonM statistic for the stationarity test. The 95th percentile of C-vonM is 0.46, which can be used to judge if the stationary test is passed

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Table B1 (*concluded*).

Aspect monitored	Diagnostic	No. of chains	Diagnostic steps	Theory and convergence criteria
			(3) For the portion of the chain passing the stationarity test, a half-width (1.96 × asymptotic standard error) test is further conducted to check if the half-width < posterior mean × ε (a small fraction, e.g., 0.1). If this test is rejected, a longer run is needed to increase the accuracy of the estimates	
Autocorrelation	Raftery and Lewis 1992	Single	(1) Suppose we wish to estimate the 2.5th percentile to within ±0.5 with probability 0.95 for each parameter (2) First, take a pilot run of at least N_{min} iterates (the minimum number of iterations needed to obtain the desired accuracy of the estimate if the draws were independent). This diagnostic then provides recommendations for an initial number of iterates to discard M (burn-in), a total number of iterates N needed to obtain the desired accuracy of the estimate for which every kth is stored, and finally a "dependence factor" $I = N/N_{min}$	The value of I measures the increase in the number of iterations needed to reach convergence due to dependence between the samples in the chain. Values of I near 1.0 indicate good mixing, whereas values of I much greater than 1.0 indicate high autocorrelation within the chain (Raftery and Lewis (1992) suggested that $I >$ 5.0 indicates problems)
Mixing of sequences	Gelman and Rubin 1992	Multiple	Run multiple chains with overdispersed starting points to see if all of the chains can converge to the same stationary distribution. CODA reports the median and the 97.5 percentile (estimated from the second half of each chain) of the sampling distribution for "shrink factor." Values of these two quantiles near 1.0 may mean effective convergence of all of the chains	The shrink factor involves both the between- and within-chain variances. It approaches 1.0 when the chains have mixed; at this point, the two variance components are essentially equal (Gelman et al. 1995)

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Appendix C. Model checking and comparison

In this appendix, we will address the important problem of model comparison and adequacy checking. Any model is necessarily a simplification of complex real-world phenomena. Hence, checking the fit of a model to data and other knowledge is always important. Nevertheless, such validation steps are rare in fisheries applications of Bayesian methods, probably due to the computational burden (Millar and Meyer 2000). We apply various predictive model evaluation techniques (Gelfand 1996) for model adequacy checking and comparison in an HBM setting. These model determination quantities can be easily calculated during the Gibbs sampling processes; therefore, routine model checking should not be too onerous.

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Cross-validation residuals

Standardized cross-validation (cv) residuals are defined as

$$\text{(C1)} \quad r_{y,t}^{cv} = \frac{c_{y,t} - E(c_{y,t}|D_{(y,t)})}{\sqrt{\text{var}(c_{y,t}|D_{(y,t)})}}$$

where $c_{y,t}$ denotes the observed count and $D_{(y,t)}$ denotes all elements of the observed data set $D = \{c_{y,t}\}$ except $c_{y,t}$. The quantities $E(c_{y,t}|D_{(y,t)})$ and $\text{var}(c_{y,t}|D_{(y,t)})$ are the expected value and the variance of $c_{y,t}$ from the cross-validation predictive distribution $p(c_{y,t}|D_{(y,t)})$. Once we have obtained a sample $\{\varphi_k^*\}$, where φ is the parameter vector and $k = 1,...,G$, from the posterior $p(\varphi|D)$ through MCMC or other sampling techniques, $E(c_{y,t}|D_{(y,t)})$ can be calculated using the following approximation for a large data set (Carlin and Louis 1996, p. 219):

$$\text{(C2)} \quad E(c_{y,t}|D_{(y,t)}) \approx \frac{1}{G}\sum_{k=1}^{G} E(c_{y,t}|\varphi_k^*)$$

where $E(c_{y,t}|\varphi_k^*) = \eta_{y,t}(\varphi_k^*)$. The variance term can be calculated using

$$\text{(C3)} \quad \text{var}(c_{y,t}|D_{(y,t)}) = E(c_{y,t}^2|D_{(y,t)}) - [E(c_{y,t}|D_{(y,t)})]^2$$

and

$$\text{(C4)} \quad E(c_{y,t}^2|D_{(y,t)}) \approx \frac{1}{G}\sum_{k=1}^{G}[\text{var}(c_{y,t}|\varphi_k^*) + [E(c_{y,t}|\varphi_k^*)]^2]$$

Here, $\text{var}(c_{y,t}|\varphi_k^*)$ is simply the variance of the counts, or σ^2.

We used the skewness and kurtosis of the standardized residuals to assess the normality of the residuals. Other diagnostic analyses traditionally performed on residuals can also be used.

Conditional predictive ordinate

We compute the conditional predictive ordinate (CPO), which is the actual value of the cross-validation predictive distribution $p(c_{y,t}|D_{(y,t)})$, for comparison of alternative model forms. The Monte Carlo estimate of the CPO (Gelfand 1996) is given by

$$\text{(C5)} \quad \text{cpo}_{y,t} = G\left(\sum_{k=1}^{G}(1/f(c_{y,t}|\varphi_k^*))\right)^{-1}$$

where

$$f(c_{y,t}|\varphi_k^*) = \left(1/\sqrt{2\pi\sigma^2}\right)\exp(-(c_{y,t} - (\eta_{y,t})_k^*)^2/2\sigma^2)$$

is the likelihood evaluated at φ_k^*. The negative cross-validation log-likelihood ($\text{ncvLogL} = -\Sigma\log(\text{cpo}_{y,t})$) (Spiegelhalter et al. 1997) is used to compare alternative models, with a smaller value ncvLogL indicating the preferred model.

Deviance information criterion (DIC)

We also use the DIC (Spiegelhalter et al. 1998) for our model comparisons. Let the deviance $D(\theta)$ be minus twice the log-likelihood of the data and θ be the parameter vector. Then

$$\text{DIC} = \text{fit} + \text{complexity}$$

where "fit" is defined as the posterior mean of $D(\theta)$, $\bar{D} = E(D)$, and "complexity" is represented by the effective number of parameters p_D, defined as $p_D = \bar{D} - D(\bar{\theta})$, where $D(\bar{\theta})$ is the deviance evaluated at the posterior expectations $\bar{\theta}$. A smaller value of DIC indicates a better-fitting model.

DIC can be readily calculated during an MCMC run by monitoring both θ and $D(\theta)$. At the kth iteration of MCMC run, we define

$$\text{(C6)} \quad D(\theta_k^*) = -2\ln(f(c_{y,t}|\theta_k^*)) = \sum_{(y,t)}(\ln(2\pi\sigma^2) + (c_{y,t} - (\eta_{y,t})_k^*)^2/\sigma^2)$$

DIC is very useful for comparing hierarchical models, where the number of parameters is not clearly defined. With non-hierarchical models, p_D is asymptotically the true number of parameters and DIC is thus equivalent to the more familiar Akaike information criterion.

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A comparison of salmon escapement estimates using a hierarchical Bayesian approach versus separate maximum likelihood estimation of each year's return

Milo D. Adkison and Zhenming Su

Abstract: In this simulation study, we compared the performance of a hierarchical Bayesian approach for estimating salmon escapement from count data with that of separate maximum likelihood estimation of each year's escapement. We simulated several contrasting counting schedules resulting in data sets that differed in information content. In particular, we were interested in the ability of the Bayesian approach to estimate escapement and timing in years where few or no counts are made after the peak of escapement. We found that the Bayesian hierarchical approach was much better able to estimate escapement and escapement timing in these situations. Separate estimates for such years could be wildly inaccurate. However, even a single postpeak count could dramatically improve the estimability of escapement parameters.

Résumé : Notre simulation compare la performance d'une approche hiérarchique bayésienne dans l'estimation des échappées de saumons à partir de données de dénombrement à une estimation indépendante de vraisemblance maximale pour chaque échappée annuelle. Plusieurs calendriers de dénombrement simulés différents ont généré des séries de données dont le contenu en information était variable. En particulier, nous étions intéressés à connaître la capacité de l'approche bayésienne d'estimer l'importance et le moment de l'échappée, les années où peu ou pas de dénombrements ont été faits après le point maximum de l'échappée. L'approche hiérarchique bayésienne s'est révélée bien meilleure pour estimer l'importance et le moment de l'échappée dans ces conditions. Les estimations indépendantes pour ces années là se sont quelquefois avérées extrêmement fausses. Cependant, même un seul dénombrement fait après le point maximum de l'échappée peut améliorer de façon spectaculaire l'appréciabilité des paramètres de l'échappée.

[Traduit par la Rédaction]

Introduction

Estimates of escapement in many salmon stocks are calculated based on aerial or foot counts. Most often, the magnitude of escapement is estimated using an ad hoc "area-under-the-curve" methodology (Neilson and Geen 1981; Perrin and Irvine 1990; English et al. 1992). Recently, likelihood-based methods have been developed that offer the advantage of a statistical framework (Quinn and Gates 1997; Hilborn et al. 1999), allowing the user to calculate the uncertainty of such estimates. Additionally, these models estimate parameters defining the timing of the escapement, useful in run reconstruction techniques (Mundy et al. 1993; Templin et al. 1996; Starr and Hilborn 1988).

Likelihood-based methods have difficulties with certain types of count data (Hilborn et al. 1999). Counts may be sparse and in particular may cease after escapement goals have been met. This can cause positive bias in estimating the magnitude of the escapement, timing, and spread in timing (Fig. 1). Hilborn et al. (1999) give an example (1990 counts of pink salmon (*Oncorhynchus gorbuscha*) in Herring Creek of Prince William Sound, Alaska) where the last count was the highest. This led to very high escapement estimates because a continued increase in abundance to a late peak could not be discounted. An area-under-the-curve approach has similar problems with such data. Usually, it is assumed that escapement declines linearly to zero over a period of one half the stream life; this may result in a large error when the biological reality differs (Hilborn et al. 1999).

An examination of more complete data from years where counts were continued longer suggested that late runs were implausible. Adding this historical information as a component of the likelihood (a pseudo-Bayesian approach) constrained the results to biologically plausible scenarios.

A natural way to incorporate "prior" information about run timing from years where count data span the peak of escapement to aid estimation in years without postpeak counts is to use a hierarchical model. In a companion paper (Su et al. 2001), we developed a hierarchical Bayesian model (HBM) and an estimation methodology that explicitly accounts for the similarity in run timing among years and applied it to estimating historical pink salmon escapement in a Southeast Alaska stream. In this paper, we use simulation to compare the theoretical performance of our hierarchical

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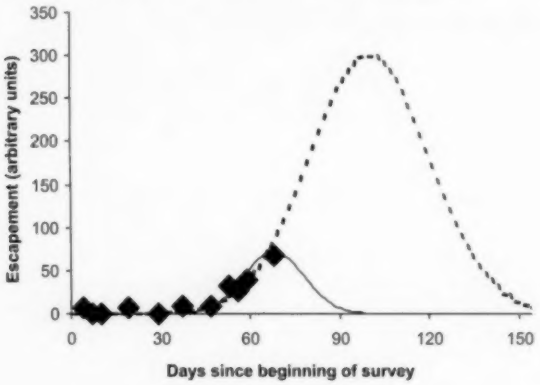
Fig. 1. Two plausible model fits to a hypothetical set of escapement counts with no postpeak information. The solid line illustrates a fit to the data that implies a smaller escapement with an earlier timing than the fit illustrated by the broken line.



Bayesian approach with the performance of nonhierarchical likelihood-based methods for escapement estimation.

Methods

A salmon spawning abundance model

In our model (details in Su et al. 2001), the number of salmon in the stream on a particular day (η_t) can be expressed as follows:

$$\eta_t = E\Phi_t \quad (1)$$

where Φ_t is the proportion of the total escapement (E) in the stream on day t. The Φ_t is the result of two processes. The first is entry of fish into the stream, which we model as proportional to a normal distribution with a mean date of M and a standard deviation in entry date of S. The second is the loss of some of the fish that are in the stream due to natural mortality. We assume that each fish entering the stream on a given date has an identical life span. This stream life is known to decline with the date of entry (Neilson and Geen 1981; Dangel and Jones 1988; Fukushima and Smoker 1997). We use an exponential decay equation to express stream life (λ_t) by date of entry t:

$$\lambda(t) = \phi_1 e^{-\phi_2(t-M)} \quad (2)$$

where ϕ_1 and ϕ_2 are two shape parameters estimated separately from independent stream life surveys and M is the mean date of arrival.

Let c_t denote the observed stream count in day t. Following Quinn and Gates (1997), we assume a normally distributed measurement error in the square root of the count:

$$\sqrt{c_t} = \sqrt{\eta_t} + \varepsilon_t \quad (3)$$

with $\varepsilon_t \sim N(0,\sigma^2)$, where σ^2 is the data error variance.

There are thus four unknown parameters for each year in this model: M, S, E, and σ^2.

Separate estimation for each year

Given particular values of M, S, and E, the model equations above can be used to predict the number of fish in the stream on any date (η_t). Maximum likelihood parameter estimates (MLEs) for a particular year can thus be estimated using a nonlinear search algorithm that selects candidate values of M, S, and E to minimize SSQ, where SSQ is the following:

$$\mathrm{SSQ} = \sum_t \left(\sqrt{c_t} - \sqrt{\eta_t(M,S,E)}\right)^2 \quad (4)$$

The bias-corrected estimate of σ^2 is obtained by dividing SSQ by the number of counts minus 3.

Confidence intervals for each parameter were calculated using a bootstrap approach (Manley 1997). A profile likelihood method (Hilborn and Mangel 1997) yielded similar results (not shown). In each bootstrap trial, residuals from the MLE fit (the differences between the square root of the counts and the square root of the predicted counts) were randomly sampled with replacement and added to the MLE predictions to create a pseudo-data set. Parameter estimates for each pseudo-data set were then calculated. This bootstrap was then repeated 1500 times. These bootstrap estimates were ordered by size, and the 15th and 85th percentiles were then taken as the lower and upper bounds of the confidence interval.

Bayesian estimation of all years simultaneously

If the behavior of the fish can be assumed to be similar in some respects from year to year (Heard 1991), simultaneously estimating the parameters of all years of data should result in more powerful inference. A hierarchical structure can be imposed on this model by assuming that the mean date of arrival and the logarithm of the standard deviation of arrival date are random samples drawn from normal probability distributions. Thus:

$$M_y \sim N(\mu_m, \tau_m^2) \quad (5)$$

$$\ln(S_y) \sim N(\mu_s, \tau_s^2) \quad (6)$$

This model is termed the M_y–S_y model. One variant that assumes that S is constant from year to year, the M_y–S model, and another that assumes M is constant, the M–S_y model, were used for a few trials.

A Bayesian framework for generating estimates from this hierarchical model is detailed in Su et al. (2001). After specifying vague priors for the hyperparameters μ_m, τ_m^2, μ_s, and τ_s^2, the sampling error in the counts (σ, assumed constant for all years), and the annual escapements $\{E_y\}$, we are able to make inferences about all parameters.

Point estimates and credible intervals for each parameter are obtained by drawing samples from the posterior distribution. A Metropolis–Gibbs sampling methodology (details in Su et al. 2001) is used to generate random draws. An initial adaptive step of 3000 iterations is used to tune the variance of the proposal distribution in order to obtain an acceptance rate of 50% for the Metropolis steps (Su et al. 2001). Then the sampler is run to generate another 15 000 random draws, of which the last 13 000 are kept. For each parameter, the median of the 13 000 values is used as an indicator of central tendency and the 15th and 85th percentiles as an indicator of uncertainty.

Simulation studies

We generated 20 years of simulated stream count data with properties similar to those of Kadashan Creek, Alaska (Su et al. 2001). We used a normal distribution with $\mu_m = 210$ and $\tau_m^2 = 25$ to generate the peak date of escapement (M_y) and a normal distribution with $\mu_s = 2.5$ and $\tau_s^2 = 0.07$ to generate $\ln(S_y)$, the spread in dates of escapement. The total escapement in each year (E_y) was generated from a uniform distribution with end bounds of 10^4 and 10^6. The simulation was then conducted as follows.

(1) Generate true values of yearly parameters: M_y^{true}, $\ln(S_y^{\mathrm{true}})$, and E_y^{true}, $y = 1,\ldots,20$.
(2) Calculate true spawner abundance by date for each year, $\{\eta_{y,t}\}$, $t = 1,2,\ldots,n_y$ using the parameter values generated in step 1.
(3) Generate a survey scheme for each year as follows. Assume that the surveys are conducted each year from day 170 (June

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Table 1. Simulation scenarios.

Scenario	Description
D_0	Escapement observed without error
All	All count data included
P1wk	Only one count made after the date of peak escapement, about 1 week later
P2wk	Only one count made after the date of peak escapement, about 2 weeks later
P4wk	Only one count made after the date of peak escapement, about 4 weeks later
5–15	First 5 years with no counts after the peak escapement; other 15 years with complete data

Table 2. Median values of RB and CV for the hyperparameters obtained from 100 simulated data sets for the M_y–S_y model under six scenarios.

	RB (%)						CV (%)					
	D_0	All	P1wk	5–15	P2wk	P4wk	D_0	All	P1wk	5–15	P2wk	P4wk
μ_m	–0.02	0.16	0.51	0.49	0.24	0.48	0.6	0.6	0.7	0.6	0.6	0.6
τ_m^2	1.11	–3.71	–5.91	–2.78	–0.85	0.59	35.8	37.9	48.3	43.4	41.5	43.5
μ_s	–0.91	0.89	1.26	1.65	0.17	0.33	2.5	2.7	3.0	2.7	2.9	2.6
τ_s^2	–3.54	5.92	1.34	–5.74	6.64	–11.74	35.5	41.2	52.2	43.2	46.4	48.7

18) to 250 (September 6) at intervals of 2–10 days (Su et al. 2001). Use a uniform distribution to generate the intervals between the surveys.

(4) Produce simulated counts using $\sqrt{c_{y,t}} = \sqrt{\eta_{y,t}} + e_{y,t}$ where $e_{y,t} \sim N(0,2200)$ (approximately the error variance estimated using the M_y–S_y model with Kadashan Creek SQRT-transformed data (Su et al. 2001)). Negative values occasionally generated by the right side of the above equation (about 8% of simulated values, mainly the smaller counts) are set to zero.

(5) HBM estimation. Using count data from all 20 years, draw samples from the posterior distribution of the parameters by running the Gibbs sampler (see the previous section). Then calculate the median and 15th and 85th percentiles of the posterior distribution of each parameter estimate. Record whether the interval between the 15th and 85th percentiles contained the true parameter value.

(6) Separate maximum likelihood estimation. Generate estimates of the annual parameters for each year using only that year's counts. Calculate the MLE of each parameter and then construct a bootstrap 70% confidence interval. Record whether the interval contained the true parameter value. To prevent extremely long searches for poorly defined MLEs, the parameter estimation was judged to have failed if the search algorithm failed to converge. This was indicated functionally when the search algorithm continued exploring values of M_y of greater than 300. Parameter estimates from these failures were not included in calculating RB or CV values below.

(7) For each estimation method, calculate the relative bias (RB) of each parameter as the percent deviation of its posterior median (or median from the bootstrap of MLE) from its true value: 100 × (median – true)/true. Also calculate a coefficient of variation-like quantity (CV) using (85th percentile – 15th percentile)/(2 × median) or (width of 70% confidence interval)/(2 × median) to quantify the precision of the parameter estimates. These two quantities are robust to outliers.

(8) Repeat the seven steps 100 times.

We summarized the RBs and CVs of each parameter across these 100 simulated data sets (2000 years in total) using their medians and 15th and 85th percentiles. We calculated coverage probabilities for confidence intervals from separate estimation and for credible intervals from Bayesian estimation.

Scenarios run

We considered six simulation scenarios (Table 1); all except the first differed primarily in the number and timing of counts taken after the peak in escapement. Scenario D_0 examined the performance of estimation absent errors in counting; instead of using the counts (c_y), we used the actual numbers of fish in the stream on those dates (η_y).

Scenario All used all the counts from throughout the spawning season. Scenario P1wk, P2wk, and P4wk contained only one count taken after the peak in escapement. In scenario P1wk, this count was the first taken after the peak, on average 1 week later. This scenario was similar to much of the data seen in Southeast Alaska pink salmon counts. In scenario P2wk, this count was taken approximately 2 weeks postpeak in the midst of the decline, and in scenario P4wk, the count was taken around 4 weeks postpeak, when few spawners remained. By comparing scenario All with scenarios P1wk, P2wk, P4wk, and the first 5 years only of scenario 5–15 (referred to below as 1st 5), we were able to determine the importance of postpeak count data and the relative importance of particular postpeak counts.

Finally, in scenario 5–15, we did not use any postpeak counts from the first 5 years of each trial but did use counts throughout the spawning season for the other 15 years; this scenario tested the ability of the Bayesian approach to use timing information from the last 15 years to salvage escapement estimates for the first 5 years. In presentations of the results of separate estimation, we lump the outcomes from these last 15 years with those of scenario All.

Results

Importance of observation error

In the absence of observation error, both separate estimation and hierarchical Bayesian methods perfectly estimated the annual parameters M, S, and E (RB = 0%, CV = 0%). However, it was still not possible to perfectly estimate the values of the hyperparameters in the HBM (Table 2). This is because the 20 years of data were essentially a finite random sample of size 20 from the hyperprior distribution. For example, the expected CV of estimating the mean μ_m from 20 random values of M_y generated according to the distribution $M_y \sim N(210,25)$ is $\sqrt{V / n} / \mu = \sqrt{25/20} / 210 = 0.53\%$. In our simulations, the median CV of our Bayesian estimate of μ_m under scenario D_0 was 0.6%, roughly the value expected (Ta-

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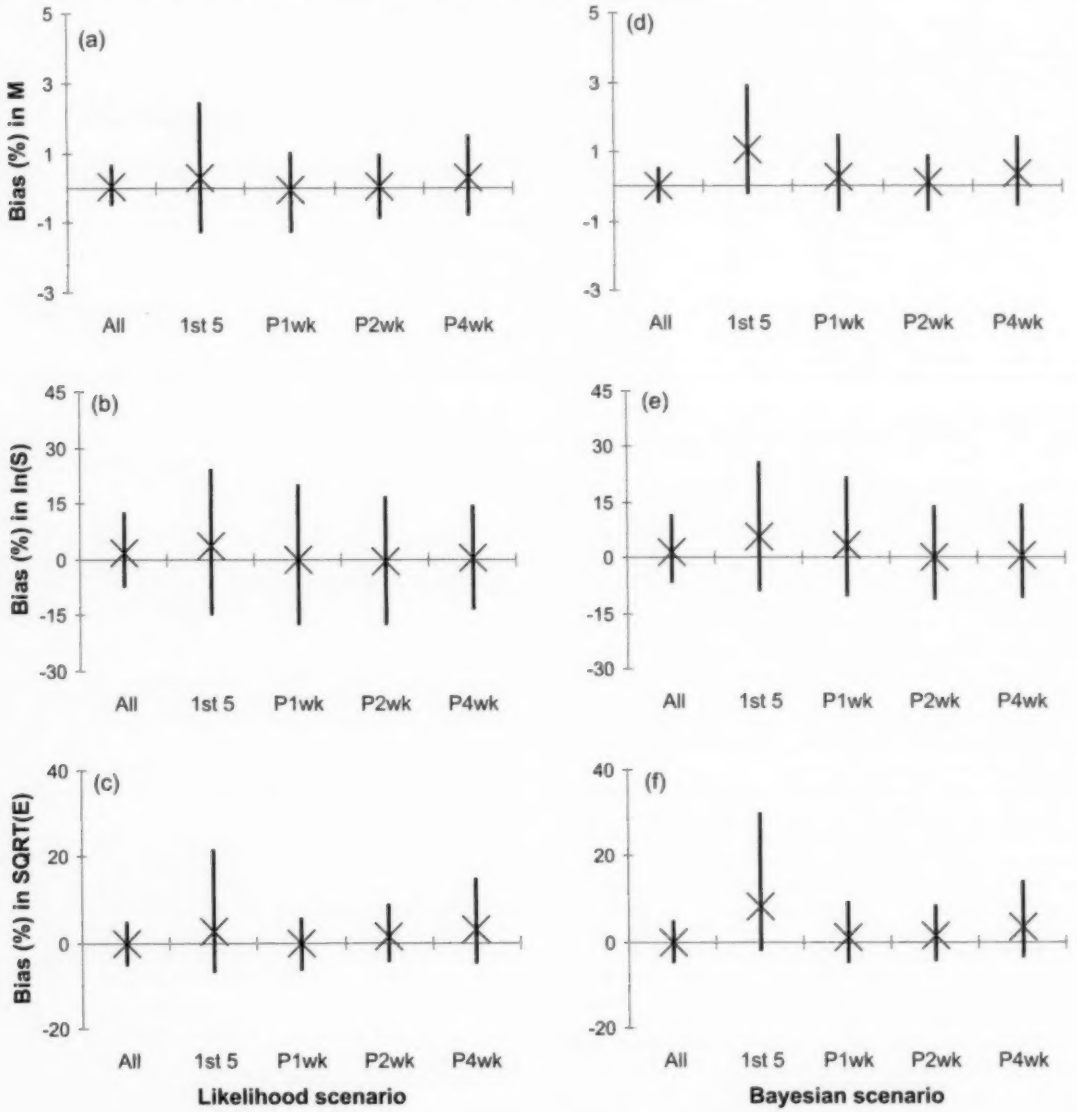
Fig. 2. RB of annual escapement timing and abundance parameters M, ln(S), and SQRT(E) for various scenarios. The ends of the vertical line are the 85th and 15th percentiles of the RB; the cross indicates the median RB. Results are shown for both (*a–c*) separate maximum likelihood estimation and (*d–f*) the M_y–S_y HBM. The label 1st 5 indicates the results from the first 5 years of scenario 5–15; the label All includes the results from scenario All plus the last 15 years of scenario 5–15.



ble 2). When counting errors were introduced, annual parameters were also no longer perfectly estimated (see below).

Ability of Bayesian methods to salvage years with no postpeak counts

Both separate estimation and HBM methods produced fairly good estimates of M, ln(S), and SQRT(E) when postpeak data were available (e.g., scenario All, Figs. 2 and 3). Estimates of escapement timing (M, ln(S)) and especially of escapement abundance (SQRT(E)) from years with no postpeak counts were considerably poorer (scenario 1st 5, Figs. 2 and 3). In part, the apparent relative precision of estimates of M is an artifact of the arbitrary scale of measurement; by assigning a value of 210 to the calendar date of the midpoint of the run, the RB and CV of M are naturally smaller than those for ln(S), whose mean is only 2.5.

With no postpeak data, both estimation methods showed positive biases (scenario 1st 5, Fig. 2). The median RB was only slightly displaced from zero, but the distribution was skewed upwards. Without postpeak data, separate estimation failed to converge to reasonable parameter estimates ($M > 300$) almost a third of the time (Table 3). Each of these

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Fig. 3. CV of annual escapement timing and abundance parameters M, ln(S), and SQRT(E) for various scenarios. The ends of the vertical line are the 85th and 15th percentiles of the RB; the cross indicates the median RB. Results are shown for both (*a–c*) separate maximum likelihood estimation and (*d–f*) the M_y–S_y HBM. The label 1st 5 indicates the results from the first 5 years of scenario 5–15; the label All includes the results from scenario All plus the last 15 years of scenario 5–15.

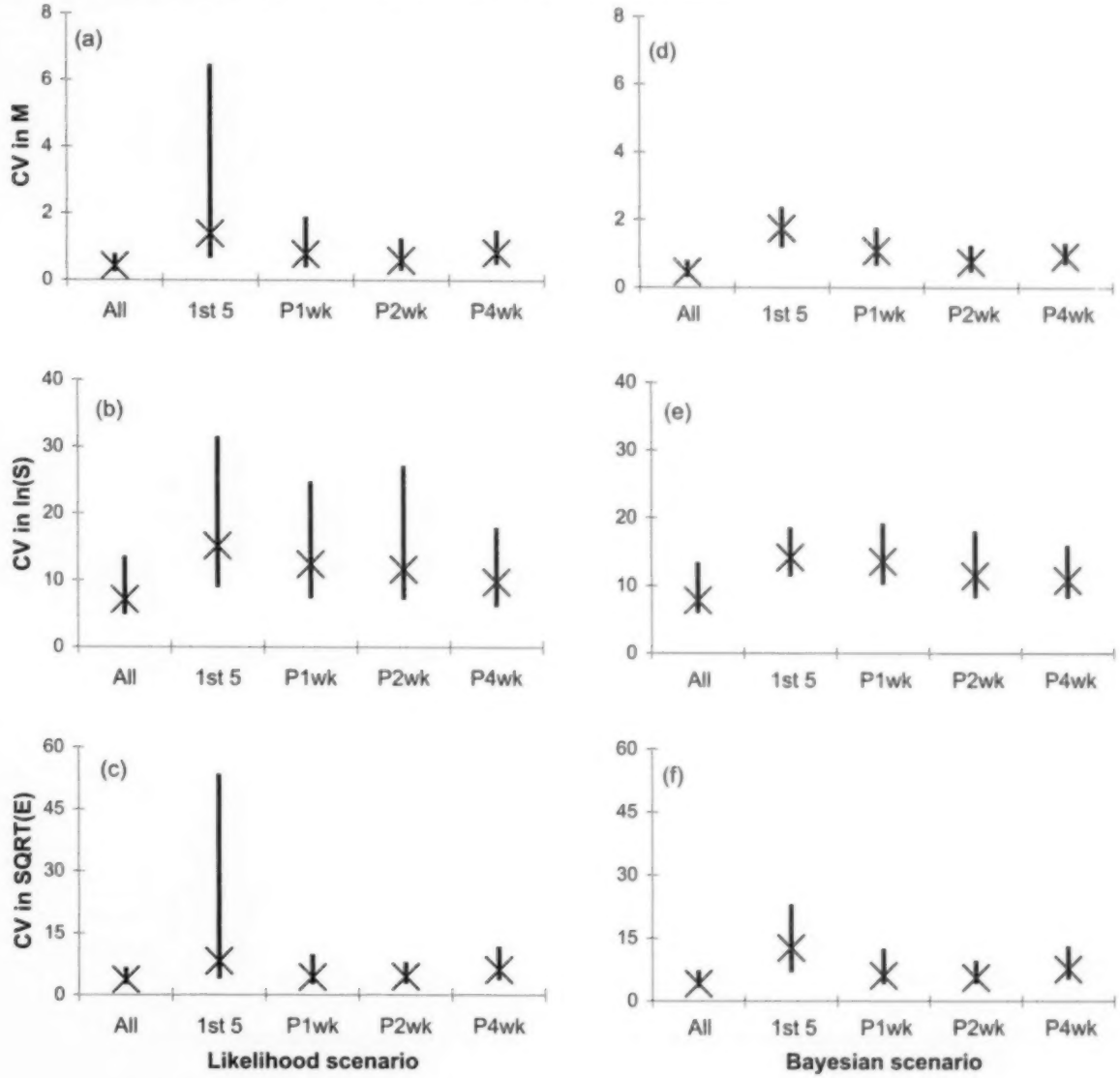

Table 3. Percentage of trials in which separate estimation "failed," i.e., the MLE of the mean date M was greater than day 300.

Trial	Failure %
All + last 15 years of 5–15	0.0
Last 5 years of 5–15	32.8
P1wk	6.6
P2wk	0.3
P4wk	0.0

trials would have resulted in a large RB. For example, for M in each "failed" trial, we would have had an RB greater than 100% × (300–210)/210 = 43%. Figure 2 thus underestimates the positive bias from using separate estimation because these frequent estimation "failures," which would have resulted in extremely large values of RB (and CV), are not included. In a separate 500 trials where we did not stop the search for parameter estimates when the estimate of M exceeded 300, the 85th percentile of RB increased to 27, 32, and 303% for M, ln(S), and SQRT(E), respectively.

Bayesian estimates also were positively biased when post-peak data were absent. Nonetheless, the HBM approach still

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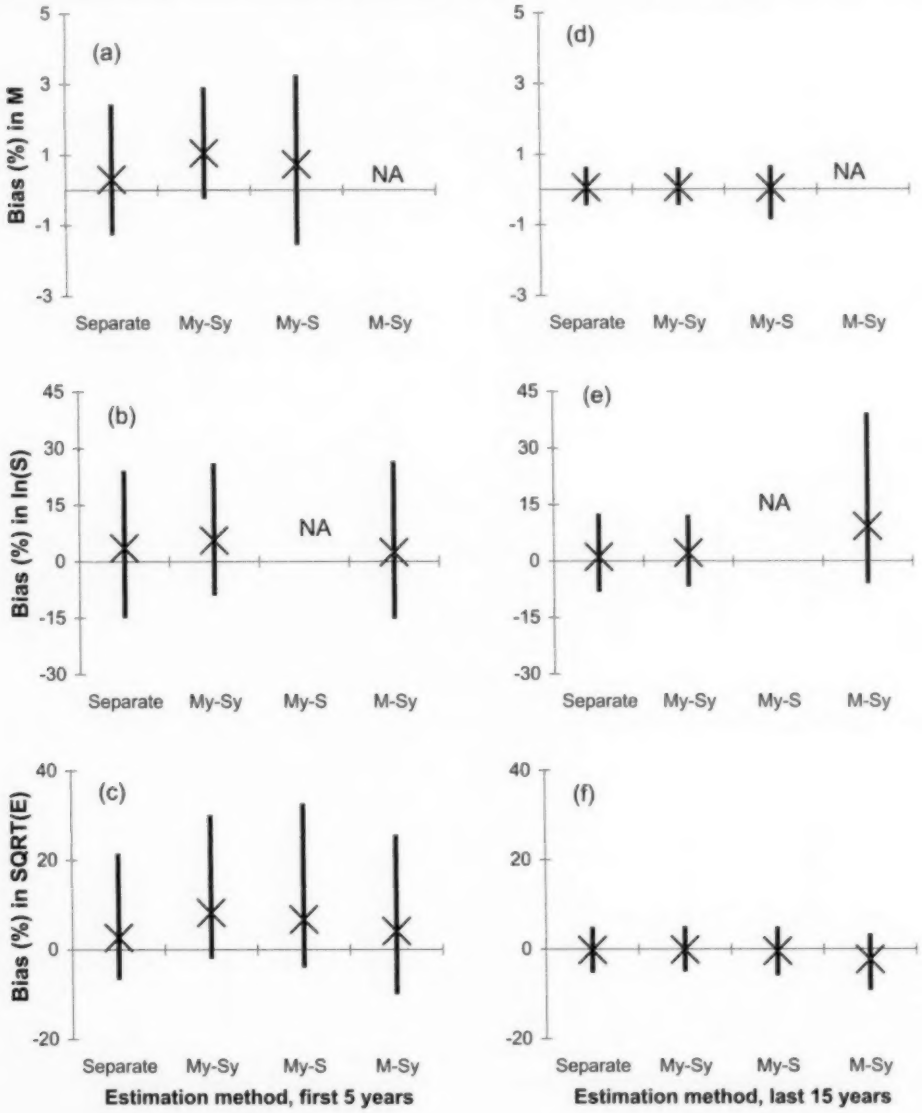
Fig. 4. RB of annual escapement timing and abundance parameters M, ln(S), and SQRT(E) for the (a–c) first 5 years and (d–f) last 15 years of scenario 5–15. The ends of the vertical line are the 85th and 15th percentiles of the RB; the cross indicates the median RB. Results are shown for both separate maximum likelihood estimation and three HBMs. NA, not applicable.



outperformed separate estimation when postpeak data were lacking (compare the width of the CV intervals for scenario 1st 5 in Fig. 3; although the median RB and CV appears larger for the HBM, this is an artifact of deleting trials where separate estimation completely failed).

Differences between the performance of M_y–S_y, M_y–S, and M–S_y Bayesian models were relatively minor compared with the differences between the HBMs and separate estimation (Table 3; Figs. 4 and 5), particularly in the CV of estimates for the first 5 years of scenario 5–15 (Figs. 5a–c). Again, for separate estimation, the 85th percentile of RB and CV for the first 5 years of scenario 5–15 is underestimated due to excluding the "failures." Performance of Bayesian estimates for the last 15 years of scenario 5–15 were comparable with those from scenario All, indicating that estimates in years when postpeak counts are available are not much affected by the uncertainty in years when they are not.

Importance of particular postpeak counts

Any postpeak data resulted in greatly improved estimates compared with those obtained when postpeak counts were lacking (Figs. 2 and 3). A single count taken 1, 2, or 4 weeks after the peak of escapement appeared to contain almost as much information about the magnitude and timing

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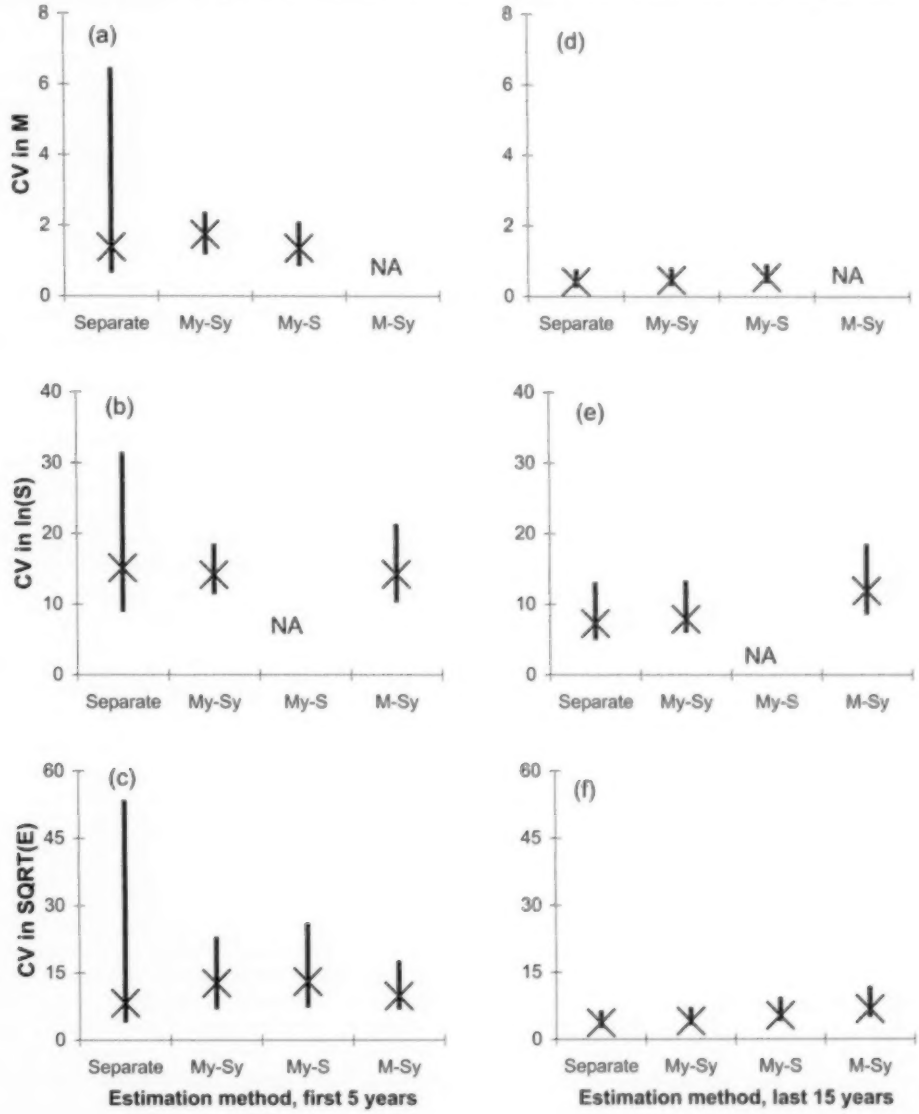
Fig. 5. CV of annual escapement timing and abundance parameters M, ln(S), and SQRT(E) for the (a–c) first 5 years and (d–f) last 15 years of scenario 5–15. The ends of the vertical line are the 85th and 15th percentiles of the CV; the cross indicates the median width of the CV. Results are shown for both separate maximum likelihood estimation and three HBMs. NA, not applicable.



of escapement as all postpeak counts. The estimated duration of the run (ln(S)) benefitted the least from the addition of a single count taken after the peak (Figs. 2*b*, 2*e*, 3*b*, and 3*e*); using the HBM approach was less likely to result in large CVs (Fig. 3*e*).

There were mostly minor differences in information content among the various postpeak counts. A count taken 1 week postpeak was least informative, possibly because the magnitude of the counting error was comparable with the expected decline in in-stream abundance, confusing interpretations. With separate estimation, a 6.6% failure rate was seen in scenario P1wk (Table 3). These were probably instances where the counting error from the postpeak count resulted in an overestimate, with the result that the series of counts did not show a peak.

Coverage properties of intervals

The coverage of 70% confidence intervals from separate estimation was poor, less than 60% when postpeak counts were available and even lower when postpeak data were absent (Table 4). The coverage of 70% Bayesian credible intervals was only slightly below 70% for most trials. One exception was the first 5 years of scenario 5–15, where the actual coverage for all three parameters was less than 65%

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Table 4. Actual percent coverage of 70% credible intervals from Bayesian estimation and 70% confidence intervals from separate estimation.

Estimation	Scenario	*M*	*S*	*E*
Bayesian	All + last 15 years of 5–15	65	70	65
	First 5 years of 5–15	61	64	59
	P1wk	65	65	70
	P2wk	65	68	70
	P4wk	65	65	65
Separate	ALL + last 15 years of 5–15	57	58	59
	First 5 years of 5–15	55	55	50
	P1wk	57	56	54
	P2wk	55	54	53
	P4wk	57	57	54

(Table 4). Nonetheless, this coverage was better than that of separate estimation. Thus, bootstrap uncertainty intervals from separate estimation may underestimate the true uncertainty, while the HBM provides nearly unbiased estimates of the uncertainty intervals.

Discussion

Our hierarchical Bayesian methods can salvage escapement estimates from years lacking postpeak counts if the assumptions are met, particularly the assumption that the variation in the timing of escapement is adequately represented by the set of years for which postpeak counts exist. This assumption is biologically credible, although climatic shifts or shifts in the relative contribution of constituent substocks could affect the timing of escapement. More likely are anthropogenic perturbations of escapement timing, e.g., changes in the timing of harvests or genetic contamination of the stock.

Estimates of escapement abundance and timing based solely on the count data for that year may yield unreasonable results if postpeak data are lacking. Unfortunately, such data sets may be common, as managers are tempted to discontinue expensive stream counts when escapement goals have been met. Just as in a linear regression, where much of the information about the slope is contained in the data with the largest and smallest x values (Draper and Smith 1981), not all postpeak counts are of equal value. Counts immediately after the peak contain the least information. A decreased count right after the peak may plausibly be interpreted as due to sampling error, with escapement possibly still increasing. Since larger escapements with later run timing are still plausible, estimates of M, S, and E are all upwardly biased. Nonetheless, any postpeak data appear to be highly valuable. Operationally, a manager will not be able to predict the date of the peak exactly. To ensure at least one postpeak count, it would be better to conduct the final count later rather than too early.

In our model, we assume that our count data are unbiased estimates of the number of fish in the watershed. In reality, count data are usually biased downwards and may have other biases as well (Dangel and Jones 1988; Bue et al. 1998; Jones et al. 1998). Any biases are necessarily propagated through the analysis and affect our estimates of escapement. Hilborn et al. (1999) dealt with this problem by explicitly modeling the bias, incorporating variability in observer efficiency based on a comparison of aerial counts and weir counts in a representative stream. Admitting uncertainty about observer efficiency greatly increased their uncertainty about the magnitude of escapement.

Our Bayesian approach could also be modified by adding parameters representing any biases. However, it is unlikely that the escapement data themselves contain enough information to reliably estimate the magnitude of any biases. In our example Southeast Alaskan pink stock, some (but not all) of the known biases were corrected prior to our use based on a calibration of aerial counts to weir counts (Dangel and Jones 1988; Jones et al. 1998). Without such calibration studies, most escapement numbers are a relative abundance index rather than an estimate of absolute numbers.

Stream life is also a potential source of bias. While we have improved on past practice by modeling the decline in stream life over the course of the season (Dangel and Jones 1988; Perrin and Irvine 1990; Fukushima and Smoker 1997), we have not incorporated interannual fluctuation in the average stream life. Such fluctuations are well documented (Ellis 1969; Dangel and Jones 1988; Bue et al. 1998), and their incorporation would undoubtedly increase uncertainty about escapement magnitude and timing. In sum, modifications to our Bayesian framework could be made to capture the additional uncertainty due to observer efficiency and stream life fluctuations. More useful, however, would be management agencies implementing prior recommendations (Quinn and Gates 1997; Bue et al. 1998; Hilborn et al. 1999) that representative streams be weired to allow annual estimates of these two factors.

The computation involved in generating Bayesian estimates of escapement can be discouraging. Obtaining point estimates of escapement is quicker in a maximum likelihood framework, since the required numerical function minimization is much faster than the numerical integration required for a Bayesian analysis. However, in calculating the uncertainty in the estimate, MLEs do not necessarily retain this advantage. The bootstrap and profile likelihood methodologies for calculating confidence intervals are not any less computationally intensive than a Markov chain Monte Carlo calculation of Bayesian credible intervals. Further, the rapid increase in cheap computing power and the development of simple numerical methods for generating samples from the posterior distribution (e.g., Gelman et al. 1995) have made Bayesian methods much more tractable.

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Nutrient-dependent recovery of Atlantic salmon streams from a catastrophic flood

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Abstract: The impact of a major flood and recovery of the stream communities under contrasting nutrient conditions were studied in two second-order streams of Sainte-Marguerite River, Quebec. A massive flood during the summer of 1996 caused extensive displacement of the stream substratum and severe reductions in the abundance of all biota: periphyton, benthic invertebrates, juvenile Atlantic salmon (*Salmo salar*), and brook trout (*Salvelinus fontinalis*) (especially in the 0+ age-class). In the postflood recovery phase, nutrient-enriched sections recovered significantly more rapidly than the nonenriched sections. After 1 month, periphyton biomass in the enriched sections had increased to five times that of the preflood levels, and after 2 months, the invertebrate communities had recovered to preflood levels. Fish densities and growth rates also returned to normal levels more rapidly in the enriched sections. Our results suggest that nutrient-rich systems are more resilient to massive disturbances, and so, nutrient enrichment may represent a viable tool for restoring nutrient-limited systems.

Résumé : L'impact d'une inondation majeure et le rétablissement subséquent des communautés lotiques dans diverses conditions de nutriments ont pu être étudiés dans deux ruisseaux d'ordre 2 du bassin de la rivière Sainte-Marguerite au Québec. Une inondation massive durant l'été 1996 a causé un important déplacement du substrat des cours d'eau et a réduit de façon significative la densité des organismes, périphyton, invertébrés benthiques, jeunes Saumons de l'Atlantique (*Salmo salar*) et Ombles de fontaine (*Salvelinus fontinalis*), particulièrement ceux de la classe d'âge 0+. Durant la phase de rétablissement après l'inondation, les sections de cours d'eau enrichies de nutriments se sont rétablies significativement plus rapidement que les sections non enrichies. Un mois plus tard, la biomasse du périphyton dans les sections enrichies avait atteint jusqu'à cinq fois la valeur d'avant l'inondation, et après 2 mois, les communautés d'invertébrés étaient retournées aux densités d'avant l'inondation. Les densités et les taux de croissance des poissons ont aussi retrouvé leurs valeurs normales plus rapidement dans les sections enrichies. Nos résultats laissent croire que les systèmes enrichis de nutriments sont plus résistants aux bouleversements massifs et donc que l'addition de nutriments peut s'avérer un outil efficace pour la restauration de systèmes limités par les nutriments.

[Traduit par la Rédaction]

Introduction

It is well known that disturbance, natural or anthropogenic, can affect the structure and function of aquatic and terrestrial ecosystems. However, it is also recognized that ecosystems often show "resistance" and "resilience" to disturbances (Webster et al. 1983; Resh et al. 1988; Biggs et al. 1999). Resistance is the ability of communities or ecosystems to withstand a disturbance, while resilience is the rate of recovery of communities or ecosystems after a disturbance (Biggs et al. 1999). The interactions between these two components could potentially determine the overall impact of disturbances on ecosystems and their recovery.

The resilience or rate of recovery, which we examine experimentally in this study, is dependent on the severity of the disturbance and its areal extent, availability and characteristics of potential colonists, heterogeneity of the disturbed area, and timing of disturbance (Sousa 1984). In the context of stream restoration, the interest usually lies in understanding how severely affected are the food resources of stream fish communities and predicting how long it may take for the disturbed habitat and the stream communities to return to their "original" condition (e.g., Gore 1985). It is not clearly demonstrated if the recovery of a disturbed food web would be dependent on the availability of nutrients or resources.

One of the most frequent natural disturbances to stream ecosystems is flooding (Fisher et al. 1982; Michener and Haeuber 1998), but the impact of large-scale floods on natural streams and subsequent recoveries are not well documented (Giller et al. 1991; Michener and Haeuber 1998). Small-scale experiments on flow (e.g., Hooper and Ottey 1988) or substrate disturbance (e.g., Johnson and Vaughn 1995) exist, but they examine only small patches or local events and are unsuitable for studying the impact of floods on a whole stream (Minshall 1988; Giller et al. 1991; Matthaei et al. 1997). Natural "experiments" represent the only viable

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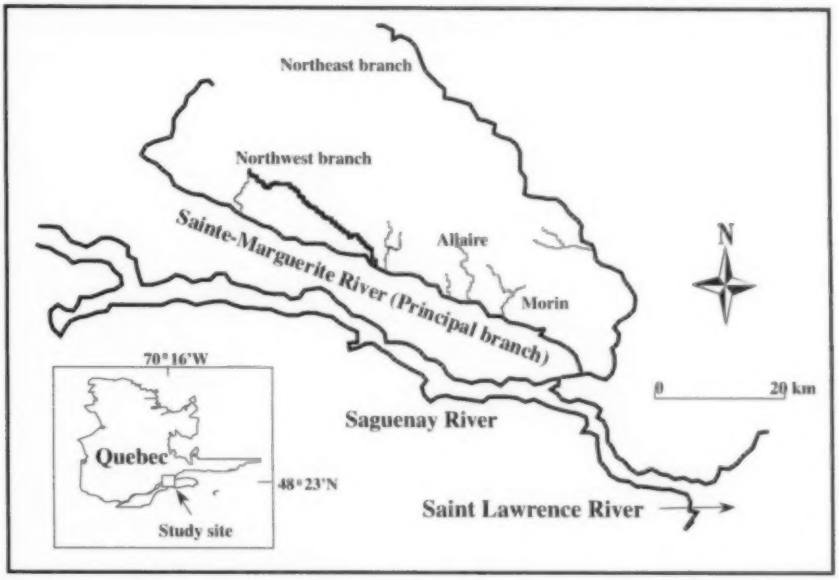
Fig. 1. Study streams (Allaire and Morin) of the Sainte-Marguerite River system, Saguenay region of Quebec.



alternative, as large-scale in situ experiments are logistically quite difficult to conduct.

One such natural experiment occurred in July 1996 while nutrient enrichment experiments were being conducted in an effort to enhance Atlantic salmon (*Salmo salar*) production, when a 100-year catastrophic flood devastated our experiments. This disaster, however, provided us a rare and unique opportunity to examine the influence of enrichment on the recovery of the stream biota. More importantly, the coincidence of the flood with our enrichment experiments allowed us to study the potential mechanisms of how nutrient – food web dynamics could be linked with the recovery of stream communities from a major disturbance.

The first objective of this study was to investigate the impact of the catastrophic flood on periphyton, invertebrate, and fish communities. The second objective was to test the hypothesis that the recovery of stream food webs is dependent on the availability of nutrients. We used 1 year of pre- and postflood data under contrasting enriched versus non-enriched conditions of two streams to test our hypotheses. A similar nutrient enrichment experiment was repeated in 1997, a year without a summer major flood. The 1997 data were used to compare the seasonal patterns for a nonflood year with those for a flood year. Our results will contribute to the understanding of the processes and mechanisms of stream food web recovery and how nutrient enrichment modulates this recovery.

Materials and methods

Experimental sites and the catastrophic flood

This study was conducted in two second-order streams, Allaire and Morin (48°24′N, 70°16′W), flowing into the Sainte-Marguerite River (Fig. 1). The Sainte-Marguerite River, located in the Saguenay region of Quebec, is an important site for the brooders of Atlantic salmon and brook trout (*Salvelinus fontinalis*) and their juveniles. Historically, this ecosystem supported a flourishing sport fishery for Atlantic salmon. Owing to a drastic worldwide decline in the salmon population during the last decades, commercial and sport fishing have been restricted and Atlantic salmon has been declared an ecologically threatened species (Saunders 1981; Mills 1989). The decline may be related to the low smolt production in the nursery streams, the degradation of spawning and rearing habitats of fish, and the overexploitation in both marine and freshwater environments (Saunders 1981; Mills 1989; Gibson 1993).

Our study streams, Allaire and Morin, varied in width from 4 to 10 m during the summer. Stream substrate was primarily gravel, pebble, and large cobbles, with sand found in small pools. Riparian vegetation along both streams was dominated by red maple (*Acer rubrum*), eastern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), white birch (*Betula papyrifera*), and grasses. The streams received sunlight during most of the day, as trees were generally about 4 m high with around a 12-m gap in forest cover at the sides of the stream channels.

These streams are nutrient poor, as indicated by the concentrations of phosphorus and nitrogen. During the summer base flow period, the concentrations of total phosphorus were relatively stable at around 5 $\mu g \cdot L^{-1}$. Total nitrogen concentrations ranged from 150 to 220 $\mu g \cdot L^{-1}$. Except during floods, the water seemed to be low in dissolved organic carbon (<6 ppm) and suspended material.

Flood disturbance is generally limited to spring (April–May) in these snowmelt streams. The discharge in summer generally ranged from 0.2 to 1.5 $m^3 \cdot s^{-1}$ and during spring floods ranged from 2 to 6 $m^3 \cdot s^{-1}$. During July 19–20, 1996, an unusually heavy rainstorm (170 mm within 36 h) produced a 100-year-magnitude flood in the Saguenay region. Besides causing more than $800 million damage to the local economy and several deaths, this flood resulted in major channel widening, boulder movements, extensive displacement of streambed, and severe erosion and landslides along the Sainte-Marguerite River network (Brooks and Lawrence 1997). In our study area, we recorded a 40-fold increase in stream discharge over the summer base flow (Fig. 2).

Nutrient additions and experimental design

The nutrient enrichment experiments were carried out from June

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23 to September 22, 1996. Phosphoric acid was added directly (using a continuous drip system) into the 1-km downstream stretches of both streams to achieve total phosphorus concentrations of approximately 20 $\mu g \cdot L^{-1}$. The flood occurred during summer when the benthic algal communities were well developed and the salmonid larvae had already emerged. As the flood occurred about 1 month after we started our nutrient enrichment experiments, the enriched and nonenriched sites within both streams were clearly different in nutrients and algal biomass. Due to the high discharge during the flood, the experimental nutrient addition was interrupted for 10 days between July 20 and 29. We restarted our experimental nutrient enrichment immediately after the water level subsided.

The basic experimental design included two similar-sized streams (Allaire and Morin) draining into the same branch of the Sainte-Marguerite River ecosystem (Fig. 1). Each stream had a 1-km upstream nonenriched section and a 1-km downstream enriched section. Within each section, we sampled in 100-m-long stretches for physical (discharge, conductivity, temperature, canopy cover, and current velocity), chemical (different forms of nitrogen and phosphorus), and biological (periphyton, benthic invertebrates, and juvenile salmon and trout) parameters. As we conducted a similar experiment in 1997, a year without a summer catastrophic flood, it was possible to validate our results of flood impacts and recoveries in 1996 with the data from 1997.

Physical and chemical properties

Stream depth was monitored twice every day and converted to discharge (Fig. 2) by constructing a calibration curve from a series of discharge measurements (Gore 1996). Current velocity was estimated with a Pygmy current meter twice every day. Temperature was monitored continuously with a temperature sensor throughout the study period. Conductivity and pH were monitored everyday. Canopy cover was estimated from overhead photographs. A camera was placed horizontally near the stream surface, lens facing up, and an overhead photograph was taken. Canopy cover was then calculated from the percentage covered by the foliage in the photograph.

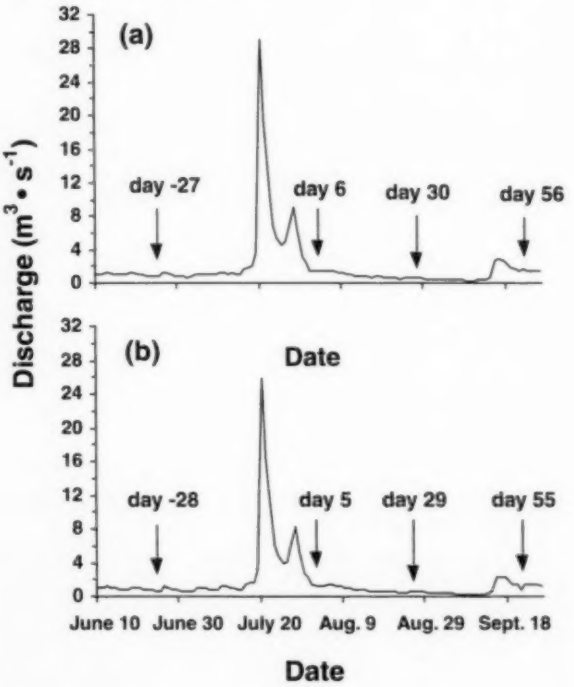
Water samples for chemical analysis were taken weekly at four stations from each of the 1-km upstream nonenriched and 1-km downstream enriched sections. Samples were transported on ice to the field laboratory in <2 h. Total phosphorus was analyzed with the ascorbic acid modification of the molybdenum blue technique (Strickland and Parsons 1972) preceded by potassium persulfate digestion under pressure (Menzel and Corwin 1965). Total nitrogen was determined after wet oxidation with peroxydisulfate digestion (Raimbault and Slawyk 1991). A Technicon autoanalyzer was used for the analyses of nutrients.

Periphyton

Rocks were randomly collected from each of the defined sampling sites. Depth, canopy cover, and current velocity were recorded at each sampling point. To remove the attached algae, each collected rock was thoroughly scraped with a wire brush into a pan containing 1 L of stream water. Six such replicate samples (from six different points within a 100-m sampling site) were collected for periphyton analysis. These samples were placed in dark polyethylene bottles, chilled, returned to the field laboratory, and kept at 4°C. In order to calculate the total surface area of the scraped rocks, the dimensions of each rock were measured with Vernier callipers (Graham et al. 1988). The estimated surface area was used to standardize the periphyton biomass. We considered one third of the total rock surface area as the planar area of stream bottom (Chantha et al. 2000) and expressed periphyton biomass per unit area of the streambed.

The periphyton samples were divided into portions. The subsamples for chlorophyll *a* analysis were filtered through glass-fiber filters (Whatman GF/C) and frozen in the dark for later analysis. Chlorophyll *a* was measured spectrophotometrically after extraction with 90% boiling ethanol followed by immersion for 24 h at 4°C in the dark and correction for phaeopigments by acidification (Nusch 1980). Subsamples for ash-free dry mass (AFDM) analysis were filtered onto preweighed filters (Whatman GF/C) and dried to a constant weight at 105°C for 24 h. The filters were then ashed at 550°C in a muffle furnace for 4 h and reweighed. The difference in weight before and after incineration was used to calculate the AFDM. AFDM represents all microbial biomass and associated organic material, while chlorophyll *a* represents the autotrophic component (i.e., viable algae).

Fig. 2. Discharge in the (*a*) Morin and (*b*) Allaire during summer 1996 and sampling days. A flood occurred during July 20–29, 1996. Days –27 and –28 represent 27 (Morin) and 28 (Allaire) days before the flood. The other days represent the number of days after the flood subsidence.



Benthic invertebrates

Six replicate invertebrate samples were taken with a Surber net (0.0625-m^2 area, 250-μm mesh size) from each of the enriched and nonenriched sections. The rocks were scrubbed and the animals were concentrated into the net. The samples were transferred into plastic jars, chilled, returned to the field laboratory, and deep-frozen at –15°C until analysis. Benthic invertebrates were identified to family, or genus if possible, counted, and measured to the nearest 0.01 mm using a dissecting microscope fitted with an ocular micrometer. The individual invertebrate dry weight was estimated using the length–weight regressions from the literature (Smock 1980; Meyer 1989) and our own site-specific estimates. Using literature information on feeding mode (Merritt and Cummins 1996) and our own observations of gut contents, invertebrates were categorized into dominant functional feeding groups (scrapers, collector–filterers, collector–gatherers, etc.) to allow the analysis of trophic structure.

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Table 1. Chemical and physical characteristics in nonenriched and enriched sections of two streams (Morin and Allaire) of the Sainte-Marguerite River.

	Morin		Allaire	
	Nonenriched	Enriched	Nonenriched	Enriched
Total phosphorous ($\mu g \cdot L^{-1}$)				
Preenriched period	4.8 (0.5) *a*	5.1 (0.6) *a*	4.5 (0.4) *a*	4.3 (0.4) *a*
Postenriched period	4.6 (0.6) *a*	20.2 (3.4) *b*	4.4 (0.6) *a*	18.6 (2.7) *b*
Total nitrogen ($\mu g \cdot L^{-1}$)				
Preenriched period	154.1 (16.8) *c*	158.6 (13.1) *c*	175.9 (20.7) *f*	181.3 (15.6) *f*
Postenriched period	213.9 (18.5) *d*	176.6 (16.4) *e*	220.5 (17.2) *g*	195.7 (21.3) *h*
pH (entire study period)	6.93 (0.65)	6.59 (0.57)	6.98 (0.56)	6.55 (0.37)
Conductivity (entire study period) ($\mu S \cdot cm^{-1}$)	31.9 (2.2)	36.1 (2.5)	29.9 (3.0)	33.2 (3.1)
Temperature (entire study period) (°C)	14.9 (0.2) (range 9.9 – 20.2)		14.8 (0.2) (range 10.5–19.6)	
Canopy cover (entire study period) (%)	39.6 (4.7)	45.6 (3.8)	31.3 (4.3)	46.7 (4.8)
Current velocity (nonflood period) ($m \cdot s^{-1}$)	0.41 (0.08)	0.36 (0.07)	0.62 (0.14)	0.47 (0.12)

Note: Mean values (±1 SE in parentheses) followed by the same letter are not significantly different (ANOVA: $P > 0.05$).

Fish

Fish densities were determined by electrofishing using population depletion estimates in both enriched and nonenriched sections (Li and Li 1996). Fish were collected during June 15–18, July 16–19, and August 24–26, 1996, and June 22–24, July 25–27, and August 21–24, 1997, and released alive after recording length and weight. Age distribution of fish was determined by using growth rings from otoliths of around 10 fish for each size-class.

Statistical analyses

To test the significance of flood impact, we used one-way analysis of variance (ANOVA) comparing the data for preflood (day –27) and postflood (day 5) dates. One-way ANOVA was also used to test the impact of enrichment (two levels, enriched versus nonenriched) on different indicator variables for four individual dates. Second-order polynomial regressions were used to determine the recovery patterns for periphyton and invertebrates. In the regression equations, the positive linear coefficients indicated the biomass and density accruals during the recovery period, while the negative quadratic coefficients indicated the population decline during the later phase of the recovery period. We also used one-way repeated measures ANOVA to validate the significance of recovery in chlorophyll *a* by using nutrient enrichment as a main factor. Systat version 8 was used for all of the statistical analyses.

Results

Physical and chemical properties

At the start of the experiment, the differences in the total phosphorus concentrations between the nonenriched and enriched sections for each stream were statistically insignificant (ANOVA: Morin, $P = 0.52$; Allaire, $P = 0.39$) (Table 1). During the course of the enrichment, the total phosphorus concentrations in the enriched sections were nearly four times higher than those in the nonenriched sections of both Morin and Allaire (Table 1). During the postenriched period, the total nitrogen concentrations were 213.9 and 220.5 $\mu g \cdot L^{-1}$ in the nonenriched sections of Morin and Allaire, respectively, while they were 176.6 and 195.7 $\mu g \cdot L^{-1}$, respectively, in the enriched sections (Table 1). The significantly lower (ANOVA: Morin, $P = 0.027$; Allaire, $P = 0.036$) total nitrogen concentrations in the enriched sections could have been due to a greater uptake by benthic algae and bacteria. The other chemical and physical characteristics (pH, conductivity, temperature, canopy cover, and current velocity) were similar in the nonenriched and enriched sections of the two streams during the entire study period (Table 1).

Periphyton

The periphyton (algae and associated organisms on rocks) biomass, as indicated by chlorophyll *a* concentrations and AFDM, was significantly reduced by the flood (one-way ANOVA using pre- and postflood data: $P < 0.001$). The average chlorophyll *a* concentrations dropped from the preflood levels of 5.7 and 4.9 $mg \cdot m^{-2}$ to postflood levels of 1.2 and 0.8 $mg \cdot m^{-2}$ in Morin and Allaire, respectively (ANOVA, $P < 0.001$) (Fig. 3). Similarly, the AFDM declined by more than 85% at all sites ($P < 0.001$) (Fig. 3). In comparison, during the same time period in July of 1997, a year without a flash flood, the chlorophyll *a* concentration and AFDM remained at around 6 $mg \cdot m^{-2}$ and 4 $g \cdot m^{-2}$, respectively (Fig. 3, second data points on solid lines). After the flood, periphyton biomass returned to its usual seasonal average levels (e.g., Fig. 3, 1997, broken lines) in both nonenriched and enriched sections. However, 1 month after the flood, chlorophyll *a* and AFDM in the enriched sections of both streams increased to fivefold and twofold of those in the nonenriched sections, respectively (Fig. 3, solid bars). By day 55–56, chlorophyll *a* levels exceeded 16 $mg \cdot m^{-2}$ in the enriched sections, while chlorophyll *a* levels in the nonenriched sections were around 5 $mg \cdot m^{-2}$ (repeated measures ANOVA: $P < 0.001$) (Figs. 3*a* and 3*b*, gray bars).

Benthic invertebrates

The flood caused 87–93% declines in the density of invertebrates from the preflood levels (around 5200 individuals$\cdot m^{-2}$ in June 1996; one-way ANOVA: $P < 0.001$) (Fig. 4). In late July, the density of invertebrates usually remained at around 4500 individuals$\cdot m^{-2}$ (Fig. 4, second data points on solid lines). The biomass of invertebrates showed similar impacts of flood in the nonenriched and enriched sections (ANOVA: $P > 0.05$). Following the flood, the biomass of invertebrates dropped from 600 to <50 $mg \cdot m^{-2}$ at all sites (ANOVA: $P < 0.001$) (Fig. 4). In the nonenriched sections of both streams, the invertebrate communities recovered only up to 30% of their seasonal average levels (e.g., Fig. 4, 1997, broken

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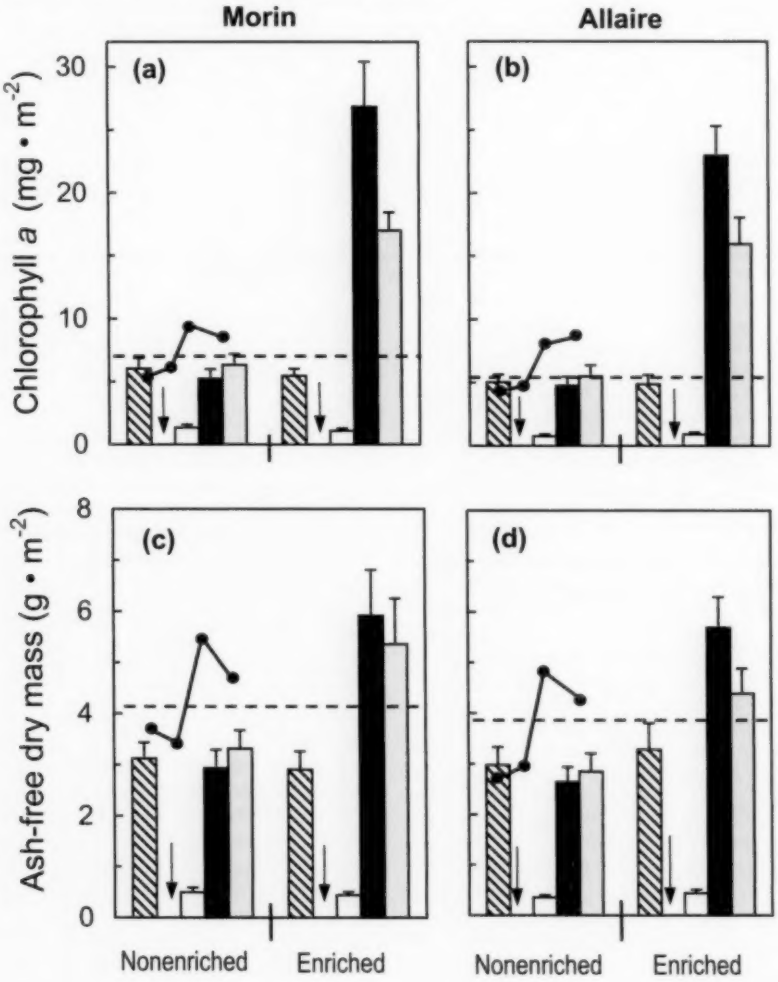
Fig. 3. Periphyton biomass, (*a* and *b*) chlorophyll *a* and (*c* and *d*) AFDM, in the Morin and Allaire under nonenriched and enriched conditions. Arrows indicate the occurrence of the flood during July 20–29, 1996. Histograms indicate the mean values ± 1 SE (n = 6) on four sampling occasions in 1996: 27–28 days before the flood (hatched bars), 5–6 days after the flood (open bars), 29–30 days after the flood (solid bars), and 55–56 days after the flood (gray bars). The broken lines represent the seasonal averages under nonenriched conditions during a nonflood year (1997, n = 40). The solid lines represent the summer seasonal pattern under nonenriched conditions in 1997 (each point is a mean of 10 observations).



lines) even 55 days after the flood. On the other hand, in the enriched sections, both the density and biomass of invertebrates reached 80–100% of their seasonal levels within only 30 days after the flood ($P < 0.001$) (Fig. 4). This recovery of invertebrates in the enriched sections was mainly due to the increases in the groups of insects that feed primarily on periphyton (Fig. 4). These functional feeding groups were collector–gatherers (mainly mayfly nymphs of Baetidae and Ephemerellidae and midge larvae of Orthocladiinae), scrapers (mainly mayfly nymphs of Heptageniidae), and collector–filterers (caddisflies of Philopotamidae and Hydropsychidae and blackflies of Simuliidae). After 55 days following the flood, the largest increase in density and biomass of invertebrates in the enriched sections was due to two groups, the scrapers and the collector–filterers (Fig. 4). This pattern was consistent for the enriched sections of both streams.

Atlantic salmon and brook trout

During the preflood period, the densities of juvenile Atlantic salmon were on an average 20 and 11 individuals·100 m^{-2} in Morin and Allaire, respectively, while the average densities of brook trout were 5 and 13 individuals·100 m^{-2}, respectively (Fig. 5, 1996). Immediately after the flood, fish abundance was very low throughout the two streams. One week after the flood, upstream movement of the surviving fish from the principal branch started to reestablish the population of both Atlantic salmon and brook trout in the streams. One month after the flood, the densities (average of all sampling

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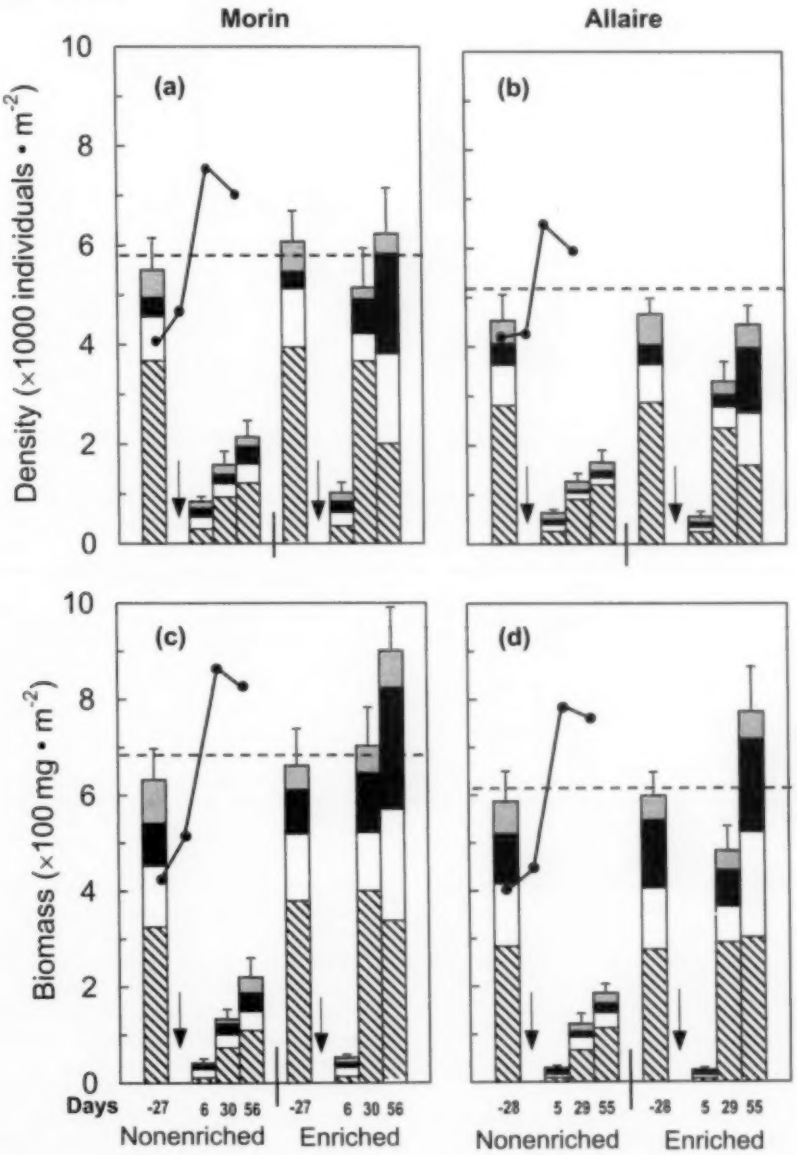
Fig. 4. (*a* and *b*) Densities and (*c* and *d*) biomass of benthic invertebrates in the Morin and Allaire under nonenriched and enriched conditions. Histograms indicate the mean values ± 1 SE (n = 6) for the total density and biomass of benthic invertebrates. Different shading in each histogram shows the contributions of various invertebrate functional feeding groups to the total density and biomass: hatched, collector–gatherers; open, collector–filterers; solid, scrapers; gray, other functional groups. Arrows indicate the occurrence of the flood during July 20–29, 1996. The broken lines represent the seasonal averages under nonenriched conditions during a nonflood year (1997, n = 40). The solid lines represent the summer seasonal pattern under nonenriched conditions in 1997 (each point is a mean of 10 observations). Days –27 and –28 represent 27 (Morin) and 28 (Allaire) days before the flood. The other days represent the number of days after the flood subsidence.



sites) returned to 76 and 56% of the preflood densities for salmon and trout, respectively (Fig. 5, 1996). A severe loss in density was seen in the 0+ age-class (Fig. 5, August 1996), and consequently, in the following year (1997), this was reflected in the relatively low density of the 1+ age-class for both salmonid species (Fig. 5, 1997). The recovery in the densities of 1+ and 2+ salmonids was distinctly better in the enriched sections (Fig. 5, August 1996). Furthermore, the weight gains of 1+ and 2+ salmonids were faster in the enriched sections than in the nonenriched sections (Table 2). By the end of August (1 month after the flood), the fish from the 1+ and 2+ age-classes were significantly heavier in

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Fig. 5. Average total densities of (*a–d*) Atlantic salmon and (*e–h*) brook trout from two sampling sites of nonenriched and enriched sections in the Morin and Allaire in 1996 and 1997. Different shading in each histogram shows the contributions of various age-classes to the total density: solid, 0+ age-class; open, 1+ age-class; gray, 2+ age-class. Arrows indicate the occurrence of the flood during July 20–29, 1996.

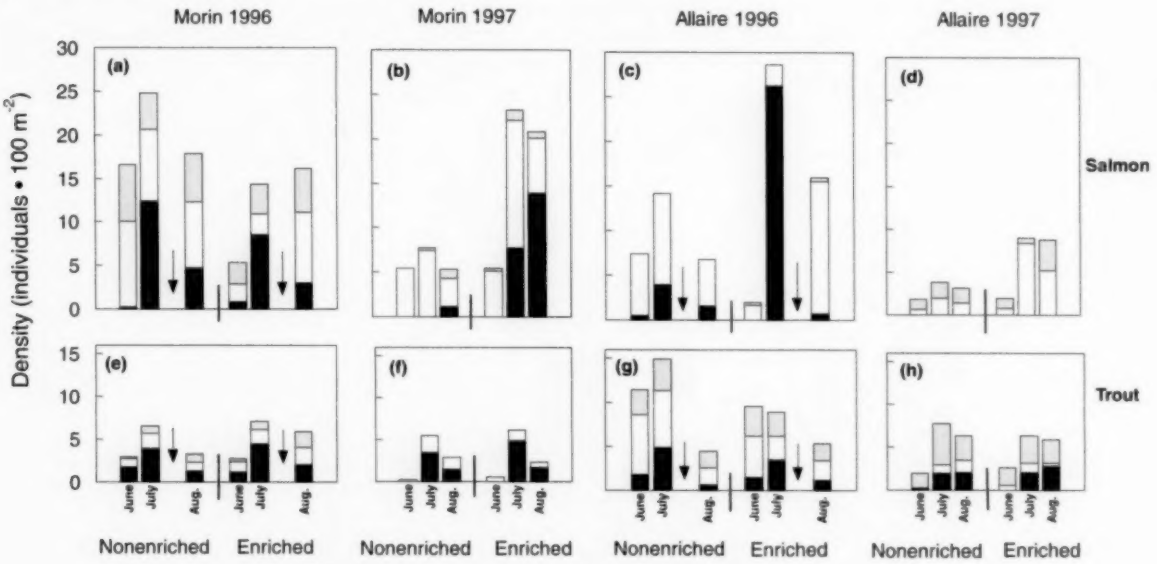

Table 2. Mean wet weights (g) (±1 SE in parentheses) of Atlantic salmon and brook trout captured in nonenriched and enriched sections of two streams (Morin and Allaire) of the Sainte-Marguerite River during August 24–26, 1996.

	Morin		Allaire	
	Nonenriched	Enriched	Nonenriched	Enriched
0+ Atlantic salmon	1.50 (0.09)	1.46 (0.07)	1.53 (0.09)	1.63 (0.19)
1+ Atlantic salmon	5.92 (0.35)	7.87 (0.56)	8.20 (0.68)	9.79 (0.36)
2+ Atlantic salmon	13.19 (0.61)	17.20 (1.59)	na	20.51 (2.87)
0+ brook trout	1.93 (0.38)	2.46 (0.32)	2.27 (0.11)	1.86 (0.12)
1+ brook trout	10.57 (1.49)	13.04 (2.04)	9.78 (0.58)	13.36 (1.10)
2+ brook trout	21.89 (2.93)	29.64 (5.18)	27.63 (3.62)	35.06 (4.57)

Note: na, not available.

the enriched sections than those in the nonenriched sections (Student's *t* test: $P < 0.01$). The mean weights of 1+ and 2+ salmon in the enriched sites were 19–33 and 30% higher, respectively, than those in the nonenriched sites. The 1+ and 2+ trout were 23–37 and 27–35% heavier, respectively, in the enriched sections than those in the nonenriched sections (Table 2).

Patterns of recovery

Based on the second-order polynomial regression analyses of chlorophyll *a*, AFDM, and the density and biomass of invertebrates as a function of days following flood, we were able to quantify the patterns of recovery by each of these food web components (Fig. 6). As indicated by the linear coefficients of the regression equations, the periphyton recovered at significantly higher rates of 1.73–2.06 mg chlorophyll $a \cdot m^{-2} \cdot day^{-1}$ in the enriched sections of Allaire and Morin compared with 0.24–0.26 mg chlorophyll $a \cdot m^{-2} \cdot day^{-1}$ in the nonenriched sections of both streams. However, due to the intensive grazing activities in the enriched sections of both streams, the concentrations of chlorophyll *a* declined after postflood day 35, as indicated by the negative quadratic coefficients of the regression equations. AFDM, an indicator of both the auto- and heterotrophic components of periphyton biomass, showed similar patterns of recovery. However, there is a greater overlap of data points for AFDM between enriched and nonenriched sections. We think that this overlap may be due to the contribution of the heterotrophic components of periphyton, which may not have responded as positively as the autotrophic components (chlorophyll *a* from viable algae). Invertebrate density increased at rates of 161–260 individuals $\cdot m^{-2} \cdot day^{-1}$ in the enriched sections of Allaire and Morin compared with 34–37 individuals $\cdot m^{-2} \cdot day^{-1}$ in the nonenriched sections. The invertebrate community also showed six to eight times faster biomass accumulation (24–40 mg dry weight $\cdot m^{-2} \cdot day^{-1}$) in the enriched sections than in the

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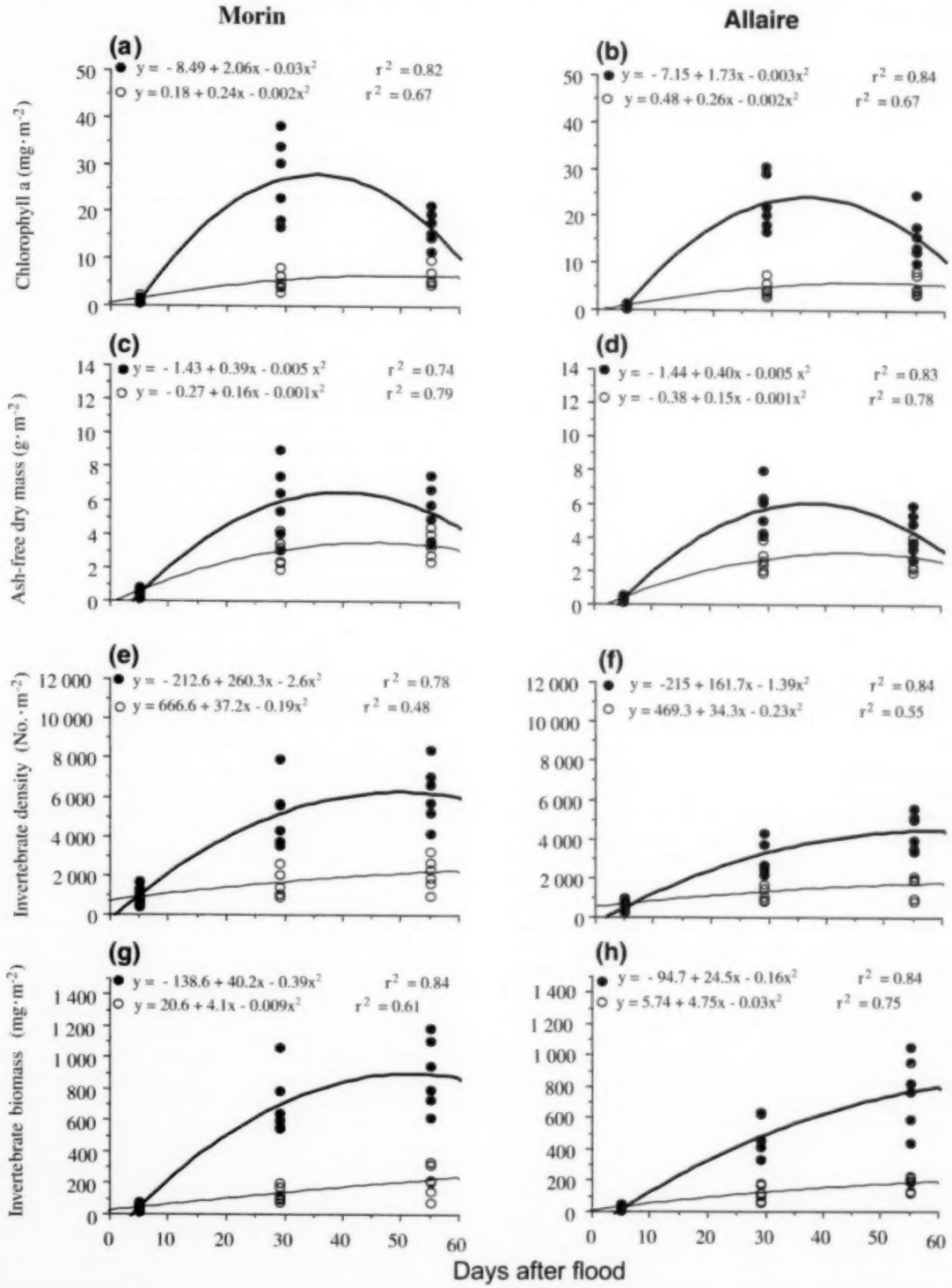
Fig. 6. Polynomial regressions of periphyton biomass, (*a* and *b*) chlorophyll *a* and (*c* and *d*) AFDM, and invertebrate (*e* and *f*) density and (*g* and *h*) biomass against days after the flood in the Morin and Allaire in 1996. Solid circles and thick lines represent data and regressions for enriched sections, and open circles and thin lines represent data and regressions for nonenriched sections.



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nonenriched sections (4–5 mg dry weight·m^{-2}·day^{-1}) of both streams (Fig. 6).

Discussion

The structure and functioning of stream ecosystems depend on the water flow patterns, availability of suitable habitat for colonization by stream biota, and the flow patterns of matter and energy along the food webs (Allan 1995). Our study suggests that a potential impact of major floods on the structure and functioning of stream ecosystems is associated with the disruption of nutrient and food web dynamics. Specifically, we demonstrate that the availability of nutrients and the resources for higher trophic levels are important determinants of the recovery of stream ecosystems from flood damage.

The time required for disturbed stream communities to recover varies widely from a few days to several months or even years (Niemi et al. 1990). Earlier studies suggested that the rate of recovery may be largely related to the severity of the flood events and the dependence on the local environmental conditions. For example, Sousa (1984) suggested that the recovery of streams depends on the magnitude and timing of the disturbance, heterogeneity of the disturbed area, and the attributes of colonists. Steinman and McIntire (1990) concluded that the recovery of periphyton after a flood depends on periphyton propagule abundance, propagule composition, and local environmental conditions (i.e., current velocity, light, nutrients, herbivory, etc.). The importance of nutrients and light for the recovery of periphyton from scouring damage has been suggested by Biggs et al. (1999) based on the results from experimental streams. Their study showed that nutrients were the most important regulator of resilience. In their experiment, periphyton under a high availability of nutrients recovered faster than periphyton under low nutrient availability. The uniqueness of our study is the integration of all of the dominant trophic linkages and their interdependence during the recovery from a major natural flood in stream ecosystems. In our study, the observed patterns of contrasting recovery of the stream food web in enriched versus nonenriched sections clearly indicate the dependence of higher trophic levels on the recovery of lower trophic levels and the associated availability of nutrients. We show that nutrient-poor streams take a significantly longer time to recover and function normally after a major disturbance. The invertebrate and fish communities did not recover in the nutrient-poor condition even 2 months after the flood. This delayed recovery from flood damage may have major implications for juvenile fish recruitment and productivity in oligotrophic nursery streams.

Nutrients, light, temperature, current velocity, and grazing pressure have been suggested to regulate periphyton biomass (Steinman and McIntire 1990; Biggs et al. 1999; Rosemond et al. 2000). Periphyton is the major food source of over 80% of the insect communities in our stream ecosystems, and these insects are the primary food of juvenile salmon and trout (Merritt and Cummins 1996; Mookerji et al. 1998). Being the lowest trophic level, periphyton showed a faster response to nutrient additions than the higher trophic levels. The additional nutrient resources in the enriched sections strongly stimulated growth rates and biomass accrual, which caused faster recovery. It is unlikely that our stream sites are light-limited, as the canopy cover on an average was 31–47% in both streams. Abundant light and continuously high temperature during the postflood period in summer may also have contributed to this rapid recovery, as also observed by Fisher et al. (1982) for Sycamore Creek, Arizona. The physical characteristics of the streams are similar in both enriched and nonenriched sections. Thus, our results suggest that the contrasting recovery patterns of periphyton and higher trophic levels are due mostly to the enhanced availability of nutrients. Steinman et al. (1991) and Mulholland et al. (1991) reported that nutrients enhance periphyton regeneration rates following light elimination and scour disturbance in laboratory streams. Valett et al. (1994) have noted the importance of nutrients for the recovery of a Sonoran desert stream from flood disturbance. The present study is likely the first in situ experiment directly demonstrating the dependence of all major trophic levels on the availability of nutrients following a massive flood.

Wallace (1990) pointed out the following mechanisms of recolonization associated with the recovery of stream benthic invertebrates from a disturbance: (*i*) migration from the deeper hyporheic zone to surface substrates, (*ii*) upstream movements, (*iii*) downstream drift from upstream or tributary areas, and (*iv*) aerial recolonization by adults. In our study, the presence of unhatched eggs as well as ovipositing adult insects during the midsummer and the migration from the hyporheic refugia soon after the flood represent the most likely recolonization processes. This is because the impact of the flood was similar throughout the streams, and thus, neither upstream nor downstream movement of invertebrates was the major mechanism for the rapid recovery. In our streams, most of the insects (e.g., mayflies and midges) typically have short generation times and various life history patterns (Niemi et al. 1990; Wallace 1990). Hence, they could rapidly increase their abundance following the enhancement of their food resources (periphyton) in the nutrient-enriched sections.

Soon after the flood, upstream movement of the fish from the connecting main river restored the fish populations in the two streams. The densities of the 1+ and 2+ age-classes for both salmon and trout reestablished relatively quickly in the nutrient-enriched sections. However, the 0+ age-class salmonids suffered more than the larger age-classes (1+ and 2+), as indicated by the very low density of the 1+ age-class in the following year (1997). Based on this observation, we are expecting a low adult return of the 1996 year-class of salmon in 2000 and 2001. As the trophic linkages were disrupted by the flood, the fish communities could not recover under nutrient-poor conditions. Thus, it seems that nutrient-poor streams and rivers can potentially loose single or multiple year-classes of fish because of the slow recovery of the lower trophic levels. On the other hand, the experimental nutrient additions that triggered a faster recovery of the periphyton produced an increased high-quality food base for the rapid increase of the major insect groups, the grazers. Since the grazing insects (mainly mayflies) are the preferred food of salmonids in our streams (Mookerji et al. 1998), we observed a higher growth of fish in the enriched sections.

In conclusion, our results show that major flood events can severely reduce the populations of stream biota and that

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nutrient-poor streams take longer to recover from such flood impacts. However, an additional source of nutrients could speed up the recovery process. We demonstrate experimentally that the recovery rates of higher trophic levels are strongly dependent on the availability of nutrients and associated recovery of periphyton. A large number of nursery streams of juvenile salmonids are often nutrient poor or oligotrophic (Gibson 1993; Allan 1995) and therefore could be highly vulnerable to episodic floods. We suggest that appropriately controlled nutrient addition could be effective in restoring the food webs and fisheries of nutrient-poor ecosystems following large floods.

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Risk aversion in allocating fishing effort in a highly uncertain coastal fishery for pelagic fish, Moluccas, Indonesia

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Abstract: The Ambonese small-scale purse-seine fishery for small pelagic fish, such as scads and mackerels, is characterised by highly variable daily catches. Fishermen involved in this fishery are therefore seriously constrained in optimising the outcome of their fishery through spatial allocation of effort. Spatial patterns in effort allocation were compared with those in catch per unit effort (CPUE), indexed by both catch weight and profit. Average CPUE indexed by catch weight differed between fishing locations by up to 14 times. However, individual fishermen could only detect such large differences after 14 days of exploratory fishing because of the high variability in daily catches. Daily decisions on effort allocation are therefore not based on maximising CPUE but on minimising operational costs and risk. A very high proportion (88%) of the fishing trips were made within 8 km of the home port, although the capacity of the purse seiners allowed for fishing in more productive areas much farther away. A 10- to 20-fold increase in operation costs (travelling and local use rights) when fishing in other areas reinforced this behaviour.

Résumé : À Amboine, la pêche à petite échelle à l'aide de sennes coulissantes de petits poissons pélagiques, tels que les chinchards et les maquereaux, se caractérise par des captures journalières très variables. Les pêcheurs engagés dans cette activité arrivent donc mal à optimiser le résultat de leur pêche par la répartition spatiale de leurs efforts. La structure spatiale des allocations de l'effort de pêche a été comparée à celle des captures par unité d'effort (CPUE), classées à la fois par masse de capture et par profit. Les CPUE moyennes, exprimées en masses récoltées, varient d'un site à un autre d'un facteur pouvant atteindre 14. Cependant, à cause de la grande variabilité des captures journalières, un pêcheur ne peut se rendre compte de telles différences importantes qu'après 14 jours de pêche exploratoire. Les décisions quotidiennes d'allocation d'effort ne sont donc pas basées sur une maximisation de la CPUE, mais sur une minimisation des coûts d'opération et des risques. Une proportion très élevée (88%) des sorties de pêche se font à moins de 8 km du port d'attache, bien que les pêcheurs aient la capacité de pêcher dans des eaux plus productives situées à des distances plus grandes. Une augmentation des coûts d'opération (frais de déplacement et permis d'opération locale) d'un facteur de 10 à 20 lorsque la pêche se fait dans des sites plus éloignés vient renforcer ce comportement chez les pêcheurs.

[Traduit par la Rédaction]

Introduction

Over the past two decades, more attention has been paid to the spatial allocation of effort by fishermen because knowledge of the behaviour of fishermen is vital for effective fisheries management. Lack of knowledge in this field is thought to be a major cause of the collapse of several fisheries (Hilborn 1985; Sampson 1991).

Fishing behaviour is governed by a variety of factors. The area over which fishing effort can be allocated is restricted by technical, environmental, and cultural factors. Although technical characteristics of the gear may change, in the short term, it is their combination with environmental conditions that determines the area where fishing is technically possible. In both artisanal and commercial fisheries, larger boats are found to have better fishing opportunities because they are more mobile (Abrahams and Healey 1990; Pet-Soede 2000) and better equipped to fish during rough weather (Hilborn and Ledbetter 1985). Existing management regulations on closed seasons and areas will further limit the resource space of fishermen to what is called the optional resource space (Ruddle and Johannes 1983).

Within an optional resource space, allocation of effort is determined through optimisation of the economic outcome of the fishery. Gordon (1953) demonstrated that if fishermen have the freedom to move between two different areas, have information on the relative catch rates to be obtained in these different areas, and attempt to maximise economic profit, the average rate of return (catch × price minus costs) should be equalised in all fishing areas. This theory has been confirmed by several authors, although the patterns in fishing effort are modified by nonmonetary costs such as the desirability of fishing areas (Hilborn and Ledbetter 1979; Hilborn and Kennedy 1992).

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The assumption of perfect information on catch rates in different areas as made in these studies cannot, however, be made in many fisheries. The information that fishermen have is based on their own experience, which can be regarded as their personal, historic "database" (Mangel and Clark 1983; Sampson 1991) or the experience that they share with other fishermen (Allen and McGlade 1986). Exploratory fishing provides additional information but implies extra costs, especially when fishing locations are far from the home port, so the value of such additional information must be weighed against the extra costs involved in obtaining it. The quality of the information is governed by the variance of, and contrasts in, catch per unit effort (CPUE) and the number of days spent exploring the potential fishing area. If variance in CPUE is high, large differences between areas, or a long period of exploratory fishing, will be needed to perceive the difference between areas. This relates to the statistical power needed to detect significant differences in catch rates (Peterman 1990).

Understanding the factors that influence existing spatial and temporal patterns in fishing effort can be useful for drafting future management plans, using the allocation of fishing effort to develop a management strategy. Information on this could be used for modelling the reaction of fisheries to management plans and the costs for the fisheries. Moreover, understanding the factors that cause uncertainty in fisheries outcome, and the extent to which these factors are recognised by the fishermen, allows a prediction of whether or not fishermen will comply with management regulations (Hilborn 1985). Fishermen who experience high levels of uncertainty in their output will have more difficulty in understanding how regulation of fishing effort will affect catch rates (Sampson 1991; Gillis et al. 1993). Indonesian purse-seine fishermen catching small pelagic fish experience extremely large day-to-day variability in resource capture (Pet et al. 1997; Pet-Soede 2000). We assume that they will have great difficulty in perceiving differences in catch rates through space and time.

The pelagic fishery in the coastal waters around Ambon and the Lease Islands, Central Moluccas, eastern Indonesia, is operated by a small- to medium-scale fleet of light fishermen dominated by purse seiners using fish aggregating devices (FADs). Due to the presence in this area of traditional local management systems for other natural resources (Evans et al. 1997), and because of a general tendency to decentralise fisheries management, one of the management objectives of the coastal and marine management strategic plan for the Moluccas is to improve the participation of fishermen in the management process (Anonymous 1998). Our contention is that the success of this kind of participation depends on the ability of fishermen to have an accurate perception of changes in resource yield and to allocate their fishing effort freely and in a rational way.

The objectives of this paper are to evaluate (*i*) whether at present, fishermen in the Central Moluccas can perceive existing spatial differences in catch rates given their day-to-day variability and (*ii*) whether they optimise their yield via the spatial allocation of their fishing effort. Spatial patterns in effort allocation are therefore compared with spatial patterns in CPUE, indexed in terms of both catch weight and net economic gain (value minus costs equals profits) per unit of effort, where the unit of effort is one night of fishing. This is done through an assessment of daily variability in CPUE and of significant spatial patterns in fishing effort and in CPUE. Because of the large day-to-day variability in CPUE, it is hypothesised that the fishermen's perception of spatial and temporal differences in CPUE is weak. This implies that allocation of fishing effort will be governed more by a fishing behaviour that minimises economic and physical risk.

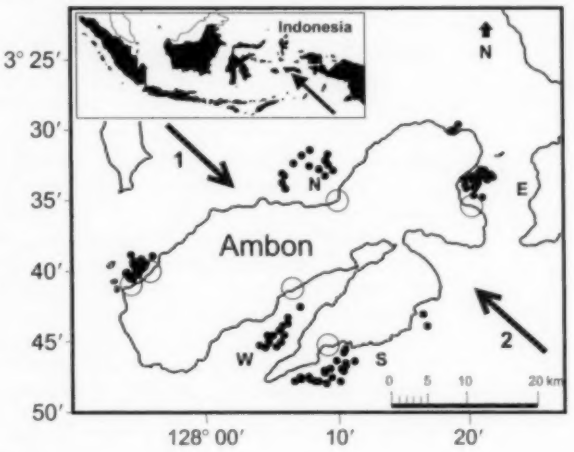

Fig. 1. Map of Ambon Island showing the locations of the main fishing villages (open circles), fishing locations used in this study, and the positions of FADs (solid circles) in the coastal waters around Ambon and the Lease Islands during October 1998. N, E, S, W, fishing areas; 1, 2, prevailing wind directions during main monsoons.

Materials and methods

Resource area and fisheries

Ambon is located at 3°40′S, 128°10′E in the Central Moluccas (Fig. 1). The island is surrounded by deep waters with minimum depths of over 200 m only a few kilometres from the coast. There are two monsoon seasons during which the large swell constrains fishing activities in the exposed part of the coastal zone. During the southeast monsoon, lasting from June to September, the prevailing wind direction is southeast, while from November to February, the wind direction is the opposite, northwest (Zijlstra et al. 1990).

There are about 20 fishing villages along the coast with an average population of 5000 per village, 2% of whom own fishing gear, varying from dugout canoes fishing with hook and line to 5- to 10-t tuna hook-and-line vessels (Anonymous 1981–1997). Many villagers are employed part-time by owners of the larger units. The deep coastal waters imply a catch dominated by pelagic fish, which form two thirds of the total fish production in coastal waters around Ambon and the Lease Islands (50 000 t in 1994) (Anonymous 1981–1997). Small pelagic fish such as small tuna (*Auxis* spp.), mackerel (*Rastrelliger* spp.), scads (*Decapterus* spp., *Selar* spp.), sardines (*Herklotsichthys* spp., *Sardinella* spp.), and anchovies (*Stolephorus* spp., *Encrassicholina* spp.) constitute 60% of the yield of pelagic fish, and more than 60% (10 782 t) of these fish are caught using purse seines.

The purse-seine fishery, a small- to medium-scale fishery with vessel sizes of around 15 m and a low level of technical innovation, is restricted to six coastal villages, each with 15–20 active purse seiners, and fishing is carried out in well-defined areas close

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to these villages (Fig. 1). The fishing techniques of the purse seiners are similar all around the island and can be described as a process split into two phases. First, fish are aggregated using traditional FADs equipped with lamps (Parrish 1999). After the fishermen have decided that enough fish have congregated below the FAD, the net is set and hauled manually by a crew of around 20 fishermen. The purse seiners make one-night trips and stay within 10 km of their home port most of the time, a distance that can be travelled within 40 min. Most of them make use of their own FADs, but the use of FADs owned either by other purse seiners or by other private owners is common. In the latter case, one third of the value of the catch has to be paid to the owner of the FAD.

Materials

To assess patterns in catch rates and in effort allocation more accurately, eight purse-seine units based at four main fishing villages with nearby fishing areas in the coastal zone of Ambon were selected (Fig. 1). Fishermen were asked to fill out logbooks noting date, fishing area, and catch weight from July to October 1998. Daily catch per species was recorded in number of baskets (18 kg) and catch rate was calculated as the catch per daily fishing trip. In addition to catch rate, technical gear characteristics such as vessel size, engine capacity, net size, and mesh size of all units were also obtained.

To assess the financial profit from a fishing trip, information on fish prices, travelling distances, and travelling costs was also gathered. Daily prices of the four main fish species caught (small tuna (*Auxis* spp.), Indo-Pacific mackerel (*Rastrelliger* spp.), roundscad (*Decapterus* spp.), big-eye scad (*Selar* spp.)) were collected from the fish market authorities in Ambon City. Because purse seiners nearly always use FADs to concentrate the fish, positions of FADs were used to identify and map the fishing areas of the purse seiners. These positions were accurately recorded during four monthly assessments at sea from October 1998 to January 1999 using a handheld global positioning system. Information about average sailing speed and fuel consumption was obtained from two purse-seine vessels.

To evaluate the observed patterns in effort allocation, they were compared with patterns found in a frame survey conducted from June to August 1997 in 20 coastal villages in Ambon to inventory the spatial and temporal allocation of fishing effort in the purse-seine fishery (J.A.E. van Oostenbrugge, unpublished data). During this frame survey, 67 purse-seine owners were interviewed, using semistructured interviews, on their effort allocation during the two monsoon periods to map their resource space through time. Fishermen were also asked which factors they thought influenced their CPUE and ultimate effort allocation.

Data analysis

CPUE corrections

Since fishermen mentioned the technical characteristics of the gear and the lunar phase as the two main factors influencing catch rates, besides spatial and seasonal patterns, these should be kept constant or corrected for. The main technical characteristics, such as boat length and the length and depth of the purse seine, varied little between the units selected for this study (Table 1), so it was assumed that their effect on catch rates was negligible.

Because the operation is based on the attraction of fish with light at night, the overall light intensity influences catch rates. The lunar cycle thus affects the temporal pattern in catch rates for these fisheries, with lowest catches during full moon (Parrish 1999). Daily catches obtained from the logbooks were used to assess the effect of the lunar phase on catch rates. As nonzero catches were lognormally distributed, the best way to correct for differences in catch rates was through a multiplicative correction factor, but the zero catches comprised 57% of the catch data, which excluded an analysis of variance for unsorted data because residuals from any analysis would not be normally distributed. Furthermore, zero catches cannot be log transformed. Therefore, the effect of the lunar phase on the probability of capture (p_c) and on the weight of the nonzero catch (C) was analysed separately.

Table 1. Technical characteristics of the fishing units from which daily catch and effort data were used.

Home port	Unit	Ship length (m)	hp	Net length (m)	Net height (m)
North	1	17	80	270	68
	2	14	80	260	50
South	1	14	80	260	50
	2	14	80	260	50
West	1	16	80	300	60
	2	18	80	300	58
East	1	22	120	300	75
	2	21	160	300	75
Mean		17	97	283	60
CV		0.20	0.32	0.08	0.19

Note: 1 hp = 745.7 W.

The effect of the lunar phase on the probability of capture was assessed using logistic regression with a logit-link function. The linear predictor $g(m)_i$ was analysed using the following model:

$$(1) \qquad g(m)_i = \log\left(\frac{p_c}{1-p_c}\right) = \beta_0 + \beta_1 l_i$$

where the βs are unknown coefficients that need to be estimated and l_i is the effect of the ith lunar phase (1–3). Three lunar phases were defined as in Pet et al. (1997): new moon, half moon, and full moon. In cases of significant effects, the 95% confidence limits of predictions were estimated to compare means of the main groups. The effect of lunar phase on the variance in weight of the nonzero catches was estimated using analysis of variance. The catches were $\log_{10}$ transformed to meet the conditions for parametric analysis of variance. The model used was

$$(2) \qquad C_{ij} = \mu + l_i + \varepsilon_{ij}$$

where $C_{ij} = \log_{10}(\text{CPUE})$, μ is the overall mean, and ε_{ij} is the error. Residuals were tested for normality and 95% confidence limits were calculated to compare means of the main groups in cases of significant effects.

The probability of capture was similar in all lunar phases, but the mean nonzero catch was 1.8 times lower during full moon than during other lunar phases ($p < 0.05$, $R^2 = 0.06$). Residuals were normally distributed ($p < 0.05$). The factor 1.8 was used to account for the full moon effect.

Profitability of allocating effort

The profitability of allocating fishing effort, starting from the different home ports in the different fishing areas, was calculated, assuming that their origin did not affect the catches obtained. Their profit differed due to differences in operation costs. The profit per trip (P) was calculated as

$$(3) \qquad P = \sum C_i v_i (1 - E_L) - E_T$$

where C_i is the catch weight of the ith species, v_i is the monetary value per unit of weight of the ith species, E_L is fees paid for the use of FADs (proportion on monetary value of catch), and E_T is expenses incurred for transport in proportion to travelling distance.

The monetary values of the daily catches were calculated from the catch composition and the price per unit weight of four differ-

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Fig. 2. Frequency distribution of $\log_{10}$-transformed catch rates in all fishing areas during the entire sampling period (July–October 1998).

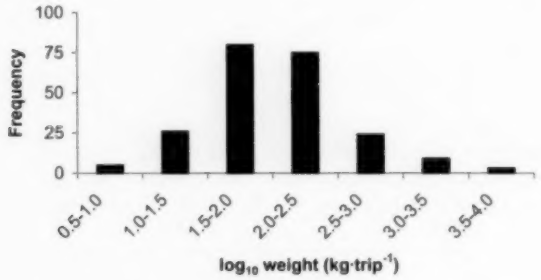
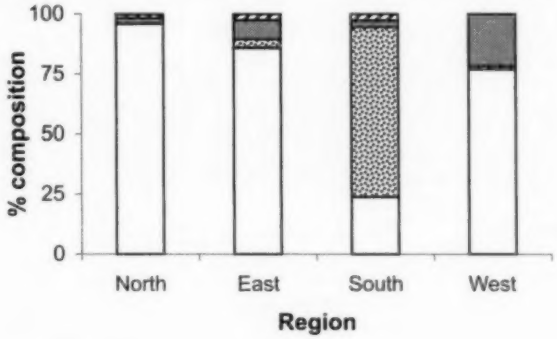


Fig. 3. Species compositions of the catches by purse seiners around Ambon per area. Hatched, sardines; gray, *Rastrelliger* spp.; stippled, *Decapterus* spp.; solid *Selar* spp.; open *Auxis* spp.



ent species categories: *Auxis* spp., *Rastrelliger* spp., *Decapterus* spp., and *Selar* spp. These four categories comprised more than 98% of the total catch, and their average retail price per unit weight was about 5000 Rp·kg^{-1} (Indonesian rupiah, 10 000 Rp = $1US, 1998). Prices per unit weight were corrected for the commission of 10% paid to the market agent and averaged over 10-day periods because of missing values on Sundays, when administrators did not work. As purse seiners only owned FADs in their local fishing area, they had to pay one third of their catch to the local FAD owner whenever they were fishing in distant areas.

The expense of travelling to and from the fishing area (monetary and time) was calculated from the distance between the home port and the fishing area and the average speed and fuel consumption of the vessels. Because of the aggregated distribution of FADs (Fig. 1), the average distance travelled to a local fishing area was estimated as the mean distance between the home port and the FADs in the local fishing area, estimated by applying Pythagorean rules to their coordinates. Distances between home ports and distant fishing areas were estimated by measuring the shortest sailing distance between them from a topographic map (Topografishe Dienst, Weltevreden, 1927, scale 1 : 100 000). Other operating costs, such as costs for lamp fuel, are negligible in comparison with these transport costs.

Patterns in CPUE

Differences in catch rates between different fishing locations were tested by month. Because of the large proportion of zero catches and the lognormal distribution of the nonzero catches, a two-step analysis seemed appropriate. However, as there are always some fish present under the FAD, the occurrence of a zero catch largely depends on the decision of the purse seiner to make a haul or not. Therefore, the percentage of zero catches does not provide true information on the occurrence of fish. Because of the nonnormal distribution of the catches, the bootstrap method was used to estimate mean catch per trip and the confidence intervals around it (Davidson and Hinkley 1997), after which the differences in catch rates and profits between fishing locations could be tested for each month using *t* tests.

Power analysis using empirically based Monte Carlo simulation

Perception of systematic differences in catch rate by the fishermen is related here to the statistical power to detect an area difference in CPUE in terms of catch weight and financial profit. We estimated the number of days of exploratory fishing, after which the probability of detecting a particular difference (power) was 0.90.

Power analysis was carried out according to the method of McAllister et al. (1992). Frequency distributions of daily catches for each fishing area and month were generated using Monte Carlo simulations based on the geometric mean and the standard deviation of the nonzero catches and on the proportion of zero catches. Differences between fishing areas were tested as described above using bootstrapping and *t* tests. These simulations were carried out 500 times, and power was computed as the ratio between significantly different events ($\alpha < 0.10$) and total number of trials. The significance level was arbitrarily set to 0.10, half as accurate as typically applied in science.

The statistical power was calculated for a range of different numbers of fishing days (5–100 with steps of 5 days). The number of fishing days needed to attain an arbitrarily set power of 0.9 was estimated using logistic regression of the power and the number of fishing days in which the number of fishing days was $\log_{10}$ transformed.

The number of days needed to detect differences in profit was estimated in a similar way as the number of days needed to detect differences in catch weight. However, in the Monte Carlo simulations, the value of the catch was used instead of the weight of the catch. This resulted in distributions of monetary values of catches from which profits were calculated from different home ports as described above.

Effort allocation

The percentage of fishing trips actually made to areas (north, east, south, west) during the two main monsoon seasons was calculated from the information obtained from the interviews during the frame survey. All fishing units were assumed to make the same number of trips. If fishermen mentioned that they were allocating effort in more than one fishing area, it was assumed that they divided their fishing trips equally over all areas mentioned.

Results

Patterns in catch rate and profit

In total, 511 catches were used for the analyses. Mean catch rate was 116 kg·trip^{-1}. The variability, expressed as the coefficient of variation (CV), in daily catches, including zero catches, was large (CV = 3.1). The percentage of zero catches for all catches combined was large, 57%. The catch frequency distributions of the nonzero catches were highly positively skewed. After $\log_{10}$ transformation of the nonzero catches, they became more normally distributed with standard deviation (SD) = 0.56 (Fig. 2). Catches were dominated by small tuna (*Auxis* spp.), except in the south, where 70% of the catch was roundscads (*Decapterus* spp.) (Fig. 3).

There were marked differences in average catch rates between fishing areas and months, despite a large day-to-day

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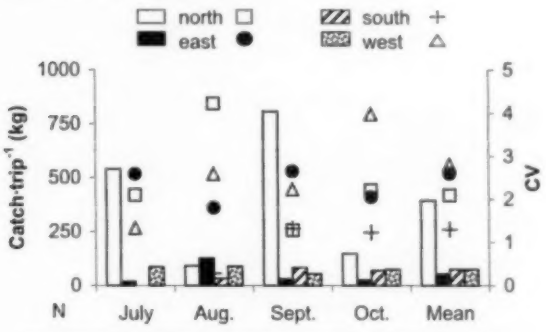
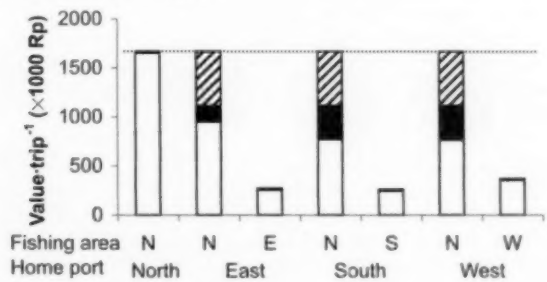
Fig. 4. Average catch rates and CVs of purse seiners around Ambon per area and month (July–October 1998). The number of observations (*N*) is given below.



N	July	Aug.	Sept.	Oct.	Mean
North	10	26	24	14	74
East	24	38	49	28	139
South	0	16	58	34	108
West	32	56	53	49	190

Fig. 5. Monetary value, local use rights (hatched), travelling costs (solid), and resulting profits (open) per trip by purse seiners from different home ports in their own or in a distant fishing area. Note the equal total monetary values per area, irrespective of the home port.



variability (Fig. 4). The average catch rate per area and month varied between 19 kg·trip^{-1} in the east during July and 807 kg·trip^{-1} in the north during September. Overall, mean catch rate in the north (395 kg·trip^{-1}) was 5.2 times as high as those in other areas, due to the large catches in the north during July (540 kg·trip^{-1}, 10.3 times as high as in other areas) and September (807 kg·trip^{-1}, 14.4 times as high as in other areas). Catch rates by month in the east were very low (19–30 kg·trip^{-1}), except during August (127 kg·trip^{-1}). The day-to-day variation in catches from the north, east, and west was very large, ranging between CV = 2 and CV = 3 during most of the months, with maximum values as high as CV = 4.2. The overall variability within these fishing areas ranged between CV = 2 and CV = 3 as well. Only in the south was overall variability smaller (CV = 1.3) and as small as CV = 0.3 during August.

Market prices of the major species differed little (Table 2). Scads (*Selar* spp.) were only 30% more expensive than the abundant *Auxis* spp., so we expect patterns for CPUE in terms of monetary value of the catch to match those in terms of weight. The value of the monthly average CPUE varied

Table 2. Daily market price data (Rp) for the species caught by the purse seiners.

Species	No. of days	Mean	SD
Selar spp.	78	5800	1900
Decapterus spp.	89	4900	1500
Rastrelliger spp.	41	4800	900
Auxis spp.	76	4500	1200

Note: 10 000 Indonesian Rp = $1US, 1998.

Table 3. Distance over sea, travelling time (out and back), and travelling costs (out and back) from the home port to the fishing area.

	Fishing area			
Home port	North	East	South	West
Distance (km)				
North	2.9	32.5	67.5	69.0
East		3.1	35.5	59.5
South			3.1	24.0
West				2.9
Travelling time (h)				
North	0.3	3.8	8.0	8.1
East		0.4	4.2	7.0
South			0.4	2.8
West				0.3
Travelling costs (Rp)				
North	14 633	163 995	340 605	348 174
East		15 643	179 133	300 237
South			15 643	121 104
West				14 633

Note: 10 000 Indonesian Rp = $1US, 1998.

between 102 000 Rp·trip^{-1} (east, October) and as much as 3 172 000 Rp·trip^{-1} (north, July). As for catch rates, CPUE in terms of monetary value in the north was at least 7.4 times as high when compared with other areas during July and was even at least 9.3 times as high during October.

Because of the small distance of approximately 3 km from the home port to the nearest cluster of FADs, travelling costs to and from the local fishing area did not exceed 16 000 Rp·trip^{-1} (Table 3). This was less then 3% of the value of their average daily catch (Fig. 5). When fishing in distant fishing areas, the large distances (24–69 km) resulted in considerable travel costs (up to 350 000 Rp·trip^{-1}) and time (up to 8.1 h). Additionally, one third of the value of the catch had to be paid to the local FAD owner. As a result of this, the costs of purse seiners from other home ports increased up to as much as 53% of the monetary value of their catch (up to 900 000 Rp·trip^{-1}) when fishing in the north.

Although travel costs and fees for the use of FADs lowered profits when fishing in distant areas, the general pattern in profits was similar to that in catch rates. For purse seiners from all ports, fishing was most profitable in the northern fishing area, especially in July and September, when average profits were higher than 1 800 000 Rp·trip^{-1}, even after subtracting travel costs. In contrast, profit to units from the northern home port would have been much lower (645 000 – 3 326 000 Rp·trip^{-1}) when fishing outside their own area

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Table 4. Minimal number of days of exploratory fishing required to prove a significant difference in catch weights and profits between local and alternative fishing areas ($\alpha = 0.10$, $1 - \beta = 0.90$).

		Alternative							
		Catch weight				Profit			
Month	Origin	North	East	South	West	North	East	South	West
Total	North		47*	56*	53*		29*	34*	31*
	East	47*		>999	>999	110*		>999	>999*
	South	56*	>999		>999	102*	>999		>999
	West	53*	>999	>999		153*	>999*	>999	
July	North		28*		44*		22*		26*
	East	28*			>999	45*			>999*
	South								
	West	44*	>999			92*	>999*		
August	North		>999	>999	>999		>999	80	>999
	East	>999		875	>999	573		61	217
	South	>999	875		>999	>999	>999		>999
	West	>999	>999	>999		>999	>999	134	
September	North		14*	17*	15*		12*	13*	12*
	East	14*		>999	>999	19*		>999	>999
	South	17*	>999		>999	25*	>999		>999
	West	15*	>999	>999		22*	>999	>999	
October	North		58	189	179		12*	15*	18*
	East	58		>999	>999	>999		>999*	241
	South	189	>999		>999	>999	71*		>999
	West	179	>999	>999		>999	37*	443	

Note: The difference should be read as going from the area of origin (rows) to a distant fishing area (columns). Positive differences are shaded and all others are negative; an asterisk means proved significant during the sampling period.

compared with fishing in their own area, except during August when profits in the east and north were almost the same.

Detectable differences in catch rate and profit

Because of the large variability in daily CPUE, few differences in CPUE between fishing areas could be proved to be significant ($\alpha = 0.10$) when fishing during the four months and with equal amounts of fishing distributed between the two areas (e.g., 52 days in each) (Table 4). Only the very large differences during September between catch rates in the northern and other areas could be perceived with the equivalent power ($1 - \beta = 0.90$) as that obtained during 1 month of exploration in both areas. Other large differences, such as those between catch rates in the northern and other areas during July, could only be proved with 28 or 44 days of exploratory fishing or more.

Profits in distant fishing areas were lowered by the extra cost of local fees and travel. Differences of CPUE in terms of profits were therefore less pronounced than those in terms of catch rates. For purse seiners from all other home ports, fishing in the north increased their overall profit, but it would take more than 4 months (100 fishing days) to prove for themselves that the difference was significant and, even then, this was mainly based on the large differences in profit made during only two months (July and September). Besides this, only fishermen from the south could gain higher profits when fishing in the east and west during August, although this difference in profit could also only be proved (based on simulations) after more than 999 days of exploratory fishing. In all other cases, purse seiners made the most profit when fishing locally. The significant differences in catch weights and profits, as proved by the field data shown in Table 4, are of minor importance because the significance level of a difference depends on the number of data available.

Patterns in effort allocation

Most of the fishermen interviewed during the frame survey mentioned that they fished in their own fishing area, especially during the monsoon with good weather conditions (Fig. 6). All trips from the northern home port were made north of Ambon during the southeast monsoon, whereas during the northwest monsoon, 65% of their trips were made in other fishing areas because weather conditions in their own area made fishing more difficult and risky. Purse seiners from the southern home ports allocated 90% of their trips during the northwest monsoon to the southern fishing area, whereas during the southeast monsoon, as many as 40% of the fishing trips were made to the western area. Effort allocation of purse seiners from the western and eastern home ports was less influenced by the monsoons. Nearly all trips (88%) made by purse seiners from the western home ports were made in their own fishing area. Purse seiners from the eastern home ports were much more mobile and made 50% of their trips in the southern fishing area and in the coastal waters of the neighbouring islands of Haruku and Seram. Patterns in allocation of daily fishing trips as recorded during the field sampling period during the southeast monsoon corroborated those observed during the frame survey.

Discussion

The results of this study clearly show that the effort allocation of purse seiners during the sampling period does not

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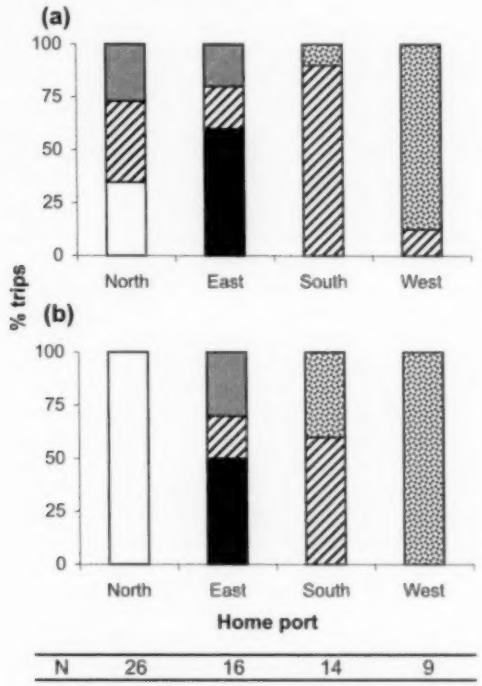
Fig. 6. Effort allocation of purse seiners from Ambon during the (*a*) northwest monsoon and (*b*) southeast monsoon as indicated during the frame survey (see text). The number of fishermen interviewed is given below. Open, north; solid, east; hatched, south; stippled, west; gray, other island.



comply with the conditions as set by Gordon (1953) for his theory on optimal effort allocation. Gordon (1953) stated that fishermen would optimise their effort allocation in order to gain the highest profits in circumstances of perfect information on catch rates and freedom to move between fishing areas. The condition of perfect information is clearly not met in this purse-seine fishery.

The assumption of perfect information about risks and profits in alternative fishing areas, used in many models predicting effort allocation in other, more certain fisheries (CV < 0.75) (e.g., Hilborn and Kennedy 1992), does not hold for the pelagic coastal fishery described here. In contrast with those fisheries, the variability of day-to-day catches in the Ambonese purse-seine fishery is as high as CV = 3.1, even when corrected for differences in technical characteristics of the gear and for lunar phase. This large variability implies a low information value of the experience of the fishermen. These fishermen can substantially enlarge the amount of information available to them, and thereby the power to distinguish between fishing areas, by gathering information from other fishermen and markets. Although this information is much cheaper than information gathered by exploratory fishing, its additional value is lower than the value of the fishermen's own experience because the variability in catch rates of other fishermen is equally large and because of possible uncertainties in circumstantial variables and possible biases.

The fishing method and the target species are important in explaining the variability of daily catches. The schooling behaviour of the small pelagic fish results in aggregated spatial distributions (Parrish 1999). The fishermen use light to attract fish, but the area around the fishing platform in which fish are efficiently affected and attracted is small (Ben-Yami 1976). Therefore, the probability of encounter between fish and light is small and the variability in the amount of fish lured is thus high. This high variability is also known for the purse-seine fisheries on small pelagic fish in other parts of the Indonesian archipelago (e.g., Pet et al. 1997).

Although fishermen were free to move into other fishing areas, operation costs when fishing in distant areas were much greater than when fishing locally. When fishing in local areas, purse seiners from all home ports only needed to catch 3 kg of fish to pay for their operation costs. Time spent on reaching the fishing area was less than 30 min·trip^{-1}, less than 5% of the total trip duration and very low in comparison with the percentage of search time of other purse-seine fisheries (70% of total trip time) (e.g., Gaertner et al. 1999). These low operation costs result from the passive nature of this fishery using FADs and lamps to trap the fish as they come by.

In contrast with the low operation costs in their local fishing area, costs of fishing in distant areas are high relative to the monetary value of the catch there. A purse seiner who fishes for a short time in another fishing area needs to hire a FAD owned by another fisherman, which costs one third of the catch obtained. Travelling costs between areas are at least 10 times as high as when fishing in their own area. When staying longer in a distant fishing area, fishermen cut down travelling costs, but housing and food for the crew have to be provided.

Other costs of fishing outside one's own fishing area that were not incorporated into the analysis are the hours spent travelling (minimum of 3.8 h). Because of the large uncertainty in the fishery, most are part-time fishermen having other occupations during the day (Acheson 1981). Longer travelling distances will reduce the time available for sleep during the night and thereby the efficiency of the fishing operation for these fishermen. Artisanal fishermen in the Spermonde Archipelago (southwestern Sulawesi, Indonesia) travel much greater distances to their fishing areas, although they also have great difficulty distinguishing between good and bad fishing areas (Pet-Soede 2000). Most of them are, however, full-time fishermen. Besides those costs related to time, the risk of accidents increases when staying longer at sea. Furthermore, the longer distance to the central market when fishing in the north can lower the quality and price of the fish, which can also be seen as extra costs of fishing in the north.

Between seasons, the costs of fishing locally vary due to weather conditions. During the northwest monsoon, fishing operations in the north are often made impossible by large waves, and the risk of damage to FADs and purse seines is high. This increases the cost of fishing in that area. Some of the fishermen anticipate this pattern and move to other areas.

The choice of where a fisherman allocates his effort ultimately depends on his evaluation of the profits and risks of fishing in different areas, as based on his own perception. We used statistical power ($1 - \beta$) as a measure of the capacity of fishermen to perceive differences in catch rates and

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profits. Although it is as yet impossible to assess the statistical power that a fisherman "uses" as a reference, we argue that it can be assumed to be high in decisions on allocating effort in distant fishing areas. Because of the large investment costs involved in exploratory fishing, it is plausible that fishermen want to maximise the probability of perceiving true differences. After each day of exploratory fishing, a fisherman will evaluate the differences between known and newly explored sites, but before deciding to allocate all of his effort in the distant fishing area, he should be sure that the difference he perceives is not merely a matter of luck (α) but corresponds to a true difference. Furthermore, this decision should increase his profit. Therefore, the critical values in the power analysis used here were arbitrarily set at $\alpha = 0.10$ and $1 - \beta = 0.90$, meaning that in 90% of the cases, true differences in catch rates are detected, and when differences are detected, 90% of those are real differences. The risk taken by the fishermen depends heavily on their economic position. Fishermen with more capital are able to take higher risks and enlarge their power to detect smaller true differences.

The above means that if a purse seiner comes from elsewhere, he would need 28 days of exploratory fishing or more in July and 14 days or more in September to have a 0.90 probability of detecting a difference in catch rates between his own fishing area and the northern area. To detect differences in profitability, he would need even more time. If there were persistent differences between fishing areas over several years, fishermen would be able to detect differences in catch rates after some time and react to them. However, during the sampling period, differences in average catch rates between areas were hardly consistent in time, so an accurate perception of catch rate levels on a scale of weeks would be needed to react accurately to the differences in catch rates. This was not possible because of the large day-to-day variability in catches. The financial risk of exploratory fishing must be large because of the substantial costs of allocation of effort in another fishing area. It is concluded that because of the large variability and the great risk involved, nearly all purse seiners allocate all of their effort within their own fishing area, close to their home port. Only the purse seiners from the east allocate some of their effort in the nearby fishing areas around neighbouring islands.

Studies on effort allocation usually refer to fisheries that are characterised either by a low variance in catch rates per fishing area or by small differences in operating costs in the different areas or by a combination of both (Gillis et al. 1993; Gaertner et al. 1999). Under such circumstances, some of the fishermen take risks and search for more profitable fishing locations, but even then, many allocate most of their fishing effort close to their home port. Individual-based models for the search behaviour of fishermen using neural networks and reinforcement learning predict that fishermen will allocate more effort close to the home port under more uncertain circumstances and that movements between areas are avoided (Dreyfus-Léon 1999). Bockstael and Opaluch (1983) modelled risk aversion in response to differences in profits of different fisheries and found this to increase with increasing uncertainty of predicted outcome and the costs of changing between the fisheries and with decreasing wealth. This agrees with the overall trend that risk takers in the fisheries are the wealthier fishermen who possess reserves to overcome periods in which catch rates are low and their fishing strategy does not pay off. Others cannot afford to take this risk and stay near their home port. The purse seiners around Ambon clearly fall into the latter category. Bockstael and Opaluch (1983) used boat size as a measure of wealth. Therefore, the larger size of the purse-seine vessels from the east might be an indication of their greater wealth and explain the fact that they are the only ones venturing into more distant fishing areas regularly. Moreover, the risk of travelling into distant fishing areas is also lower for larger fishing vessels.

The results of the recent study relate to two major objectives in the Indonesian coastal and marine management strategic plan (Anonymous 1998): the development of a community-based fishing industry that is ecologically sustainable and the improvement of community participation in the management and planning of the coastal and marine areas. The success of this kind of co-management depends on the perception of the fisherman of the state of the stocks. When fishermen perceive a downward trend in their CPUE and define that as their problem, they will be more willing to co-operate in a new management strategy. Apparent results of such a strategy will stimulate the fishermen to obey management rules. The amount of data available to the fishermen to detect such long-term trends is larger, especially when communication between fishermen is good, and so as a community, they will have large power to detect differences. The information flow through these communication networks is a topic for future study on the perception of spatial and temporal patterns in resource outcome. Nevertheless, the highly variable CPUE in the pelagic fishery, as experienced by an individual fisherman and as analysed here, will obscure the perception of trends and with that make it more difficult for him or her to judge the effectiveness of any management strategy, when compared with other, less variable fisheries. Co-management with a goal of protecting future stocks might therefore not be easily made effective in fisheries such as the purse-seine fishery around Ambon and the Lease Islands.

Acknowledgements

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A paleolimnological assessment of the effects of post-1970 reductions of sulfur deposition in Sweden

A.S. Ek and T. Korsman

Abstract: Analysis of diatoms in sediment cores from 10 acidic (pH < 6) lakes in southern Sweden shows that eight of the lakes have acidified after 1950, while two lakes have not significantly acidified. However, since the 1970s, sulfur deposition has decreased by 50%, and lake water chemistry monitored since 1983 shows an initial reversal of acidification. However, the diatom data do not indicate that a general recovery in pH has occurred yet. The diatoms show that a small recovery has occurred in only one lake (pH increase from 4.7 to 4.9). The 10 lakes vary in total organic carbon content from 2 to 17 mg·L^{-1}. According to the diatoms, the lakes with high total organic carbon (>9 mg·L^{-1}) have not acidified as much as the lakes with lower total organic carbon (<7 mg·L^{-1}). We ascribe this difference in response to acid deposition to the buffering capacity of organic acids. Knowledge of the role of organic acids when combined with anthropogenic acid deposition is important in predicting responses to decreasing acid deposition and the time scales required for recovery. Paleolimnological methods are shown here to provide valuable information for these purposes as well as to provide a long-term perspective on lake acidity changes needed for the evaluation of recovery.

Résumé : L'analyse des diatomées dans des carottes de sédiments de 10 lacs acides (pH < 6) du sud de la Suède indique que huit des lacs se sont acidifiés après 1950, alors que deux autres n'ont pas subi d'acidification significative. Depuis les années 1970, les retombées de soufre ont diminué de 50%, et un suivi de la chimie des eaux des lacs depuis 1983 révèle un renversement initial de l'acidification. Néanmoins, les données sur les diatomées ne montrent pas encore de redressement général du pH; en fait, elles indiquent une faible récupération dans un seul des lacs (augmentation du pH de 4,7 à 4,9). Les 10 lacs diffèrent dans leur contenu en carbone organique total de 2 à 17 mg·L^{-1}. D'après l'étude des diatomées, les lacs à haute teneur en carbone organique total (>9 mg·L^{-1}) ne se sont pas acidifiés autant que les lacs avec peu de carbone organique total (<7 mg·L^{-1}). Cette différence de réaction aux précipitations acides nous semble due au pouvoir tampon des acides organiques. Une connaissance du rôle des acides organiques en présence des précipitations acides anthropiques est nécessaire pour pouvoir prédire les réactions à la diminution des précipitations acides et le temps requis pour la récupération. Les méthodes paléolimnologiques fournissent donc des données précieuses pour ces prédictions et elles donnent aussi la perspective à long terme des changements d'acidité des lacs nécessaire pour pouvoir évaluer la récupération.

[Traduit par la Rédaction]

Introduction

The adoption of protocols included in the Convention on Long-Range Transboundary Air Pollution (CLRTAP) has resulted in decreasing sulfur emissions in Europe (United Nations Economic Commission for Europe 2000). Acidification has affected large parts of Europe, especially Fennoscandia, and the reduction in emissions is expected to lead to an improvement of the acidification status of surface waters. However, key questions remain to be addressed. How fast will the ecosystems recover from acidification, what magnitude of reductions is needed for the reversal of lake acidification, and how fast will the response of organisms in the lakes be to changes in water chemistry? Answers to questions like these are important for understanding the anticipated recovery from acidification. Research on recovery has encompassed studies involving chemical and biological monitoring of responses to the post-1970 decrease in emissions (e.g., Keller et al. 1992; Ek et al. 1995; Stoddard et al. 1999), the manipulation of ecosystems such as roof building and (or) various catchment treatments (e.g., Schindler et al. 1991; Wright et al. 1993; Hultberg and Skeffington 1998), simulations (e.g., Skeffington and Brown 1992; Jenkins et al. 1998; Moldan et al. 1999), and paleolimnological analyses of lake sediment cores.

Paleolimnological methods have been important in establishing the time scales and extent of acidification as well as its causes, and diatoms have played a crucial role in these investigations (Battarbee et al. 1999). Diatoms respond quickly to changes in lake acidity, and studies of recovery using subfossil diatoms in lake sediments have been performed in North America (Dickman and Fortescue 1991; Smol et al. 1998), the United Kingdom (Battarbee et al.

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1988; Allott et al. 1992; Juggins et al. 1996), and Sweden (Ek et al. 1995; Ek and Renberg 2001).

Sulfur deposition in Sweden peaked in the 1970s, and following national and international reductions in emissions, deposition has decreased by at least 50% in southern Sweden (Warfvinge and Bertills 2000). This has resulted in the pH in precipitation increasing during the 1990s (Warfvinge and Bertills 2000). Since sulfur emissions from central Europe and the British Isles have been the major source of sulfur deposited in Sweden, there is a strong gradient of sulfur deposition, decreasing from south to north, and the largest decreases have occurred in the most southern part of Sweden. Nitrogen deposition peaked around 1990, and since then, a small decrease has been observed (Warfvinge and Bertills 2000).

Although lake acidification was first detected in the 1960s in Sweden, national programs for monitoring lake water chemistry did not start until 1983, and in 1989, a number of lakes were selected as reference lakes for temporal monitoring of both their chemistry and their biology. However, knowledge concerning the conditions of the lakes prior to the monitoring program is limited.

Here, we present results from paleolimnological analyses of 10 national reference lakes in southern Sweden. Diatom analyses were used to study acidification trends over the last few hundred years and to assess the responses to the reduced acid deposition that have occurred since the 1970s. Special attention was paid to whether lakes with low total organic carbon (TOC) concentrations have developed differently than those with high TOC concentrations.

Material and methods

Study sites

The 10 study lakes (Fig. 1) were chosen from the unlimed national and regional reference lakes, numbering about 190, included in the lake monitoring program being conducted by the Swedish Environmental Protection Agency. The water chemistry has been monitored three to four times a year since 1983–1984. Since 1989, six of the 10 lakes have been included in a subset of reference lakes that have been more intensively studied, i.e., they have been subjected to both biological monitoring and a higher frequency of chemical analysis. The lakes are small (0.1–1.7 km^2 in area) and fairly shallow (maximum depth 3.8–36 m). Data on water chemistry parameters between 1983–1984 and 1997 were obtained from the Department of Environmental Assessment, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden. The water chemistry data and information on the chemistry analyses are available at the homepage of the Department of Environmental Assessment (www.ma.slu.se).

Sediment coring and paleolimnological analyses

Sediment cores 20–39 cm in length were taken with a freeze corer in the deepest part of the lakes. Örvattnet was cored in spring 1994 (Ek et al. 1995) and the others in 1997. The only exception was Härsvattnet, which was cored in the summer of 1997 using an HTH gravity corer (HTH-Teknik, Vårvägen 37, SE-976 31 Luleå, Sweden).

The freeze cores were subsampled in 2-mm intervals to a depth of 5 cm below the sediment surface, while the remainder was sliced in 5-mm intervals to a depth of 10 cm and thereafter in 1-cm intervals. The gravity core was sampled in 2.5-mm intervals down to 5 cm and thereafter in 5- and 10-mm intervals. Diatom slides were prepared by boiling the sediment samples in H_2O_2 (Renberg 1990). In near-surface sediments, diatom analyses were done at close sample intervals to detect possible recent acidification and recovery, while assessment of preindustrial conditions were done at a lower resolution. Prior to analyses, the slides were randomly numbered so that the sediment levels that they represented were unknown to the analyst. Between 400 and 500 diatom valves were counted on each slide. The taxonomy followed the conventions adopted by the diatomists participating in the Surface Water Acidification Program (SWAP) (Stevenson et al. 1991), and the keys provided by Krammer and Lange-Bertalot (1986–1991) were used for a few species that had not been recorded at the SWAP sites.

The diatoms in sediments of four of the lakes had been analyzed previously, and for these, only the top 5 cm of the present cores was analyzed and then correlated with the earlier cores by comparing the diatom assemblages. The 1994 Örvattnet core was correlated with a freeze core from 1988 (Ek et al. 1995), the 1997 Härsvattnet core with a freeze core from 1992, the 1997 Lilla Öresjön core with a freeze core from 1986, and the 1997 Brunnsjön core with a freeze core from 1992 (I. Renberg and T. Korsman, unpublished data).

Changes in lake water pH were inferred from the diatom assemblages using the SWAP data set (Stevenson et al. 1991) and the program WACALIB 2.1 (Line and Birks 1990). The SWAP data set consists of measured water chemistry values and data on diatom assemblages in the surface sediments from 167 lakes in Sweden, Norway, and Great Britain.

Spheroidal carbonaceous fly-ash particles (SCP), which are produced when fossil fuels are burnt, were analyzed to provide approximate dates for the sediment cores and for assessing the deposition load of airborne pollutants. Earlier paleolimnological studies have revealed that there was an appearance of SCP in the late nineteenth century and that there was a postwar increase from about 1950, a peak at about 1970, and then a decline due to the "oil crisis" and efforts to clean smoke (Wik and Renberg 1996). SCP were prepared and analyzed according to a method described by Renberg and Wik (1985). The SCP analysis in this study was primarily intended for use as an indirect dating tool, i.e., to identify the strata representing the late nineteenth century appearance and postwar increase in SCP. Not all the sediment cores were analyzed for SCP all the way up to the sediment surface. However, in the lakes with a complete SCP record, the SCP profiles also provided a complement to the lake water sulfate data when assessing the deposition of airborne pollution.

Multivariate statistical analysis

The computer program CANOCO (Ter Braak 1990) was used to analyze changes in the diatom flora. All multivariate analyses were performed on diatom data at the species, or variety, level. Rare species, i.e., those occurring in less than three samples, were removed prior to analysis. First, detrended correspondence analysis (DCA) was used to test the gradient length. The decision between using a linear or nonlinear approach for further multivariate analyses was based on the gradient length of the first axis from the DCA. For the whole group of 10 lakes, the DCA indicated that there was a nonlinear response (gradient length = 2.7 SD); thus, a nonlinear approach (correspondence analysis (CA)) was used to differentiate between the diatom responses in the different lakes.

To study more subtle changes in the diatom flora, in this case to find indications of recovery from acidification such as a return to communities with a species composition similar to the pre-acidification assemblages, individual ordination analysis was performed for each lake. DCAs performed on the individual lakes indicated linear diatom responses. In four of the lakes, the gradient length of the first axis was <1.5 SD, while six of the lakes had a gradient length of 1.6–1.9 SD. Thus, a linear approach (principal component analysis (PCA)) was used to study the floristic changes within each lake.

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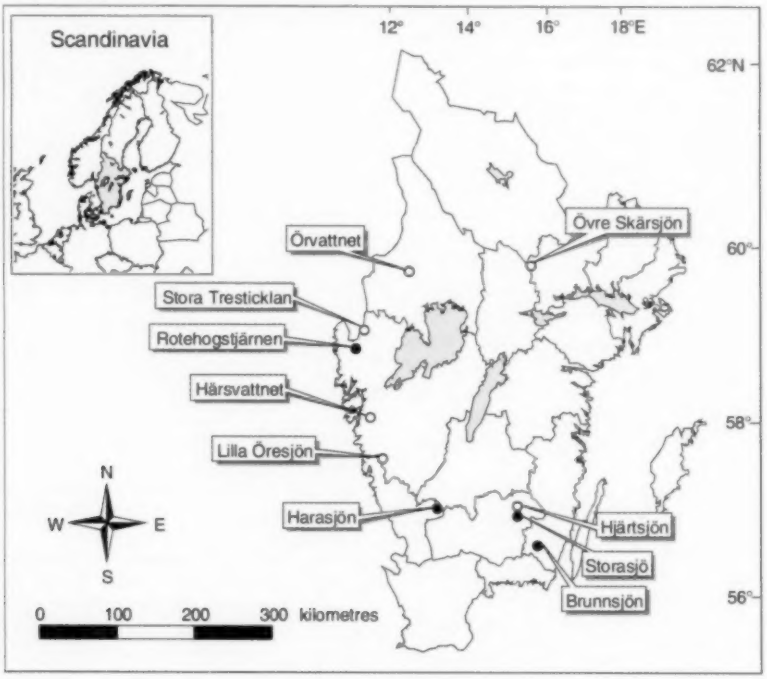
Fig. 1. Location of the 10 study lakes in southern Sweden. Lakes marked with solid circles are lakes with high TOC, and open circles represent lakes with low TOC (see text).



Results

Water chemistry

The study lakes are acidic (pH 4.5–5.3), with TOC concentrations ranging from 2 to 17 mg·L^{-1} (Table 1). Since the lakes in this study were subjected to variable within-year sampling frequencies, annual means are presented to serve as an evaluation of the paleolimnological data. In Fig. 2, the lakes have been grouped according to the lake water quality criteria set by the Swedish Environmental Protection Agency (1999) in which <8 mg TOC·L^{-1} is considered low to very low and >8 mg·L^{-1} is considered moderate to very high. Thus, six lakes were classified as having low TOC levels (2–6.7 mg·L^{-1}) (Table 1) and four lakes as having high TOC levels (9.4–17 mg·L^{-1}) (Table 1). As a result of the reductions in sulfur deposition, the sulfate concentrations decreased in most of the lakes during the 14–15 years of monitoring. Sulfate concentrations decreased by 25–35% in the low-TOC lakes and by 15–30% in three of the high-TOC lakes between 1984 and 1997 (Figs. 2*a* and 2*c*), but did not fall in the fourth high-TOC lake (Fig. 2*c*). The four high-TOC lakes show larger between-year variations as well as larger seasonal variations in sulfate content compared with the low-TOC lakes. The within-year sulfate variation (calculated as the mean difference between the highest and lowest sulfate concentrations during each year for the period 1984–1997) was 9–23 μequiv.·L^{-1} for the low-TOC lakes and 40–70 μequiv.·L^{-1} for the high-TOC lakes.

The base cation concentrations (not shown) generally also decrease (15–40% in the low-TOC lakes and 5–20% in three of the high-TOC lakes). In the high-TOC lakes, the base cation concentration is greater than the sulfate concentration, while in the low-TOC lakes, it is generally the same or less than the sulfate concentration, except in Övre Skärsjön, where it is greater than the sulfate concentration.

The mean total aluminum concentration (not shown) for the lakes during the last two years (1996 and 1997) was 247 μg·L^{-1} (range 136–472 μg·L^{-1}). There were no significant changes in the aluminum concentrations between 1984 and 1997, except for Härsvattnet, where aluminum decreased by about 45%, and Brunnsjön, where aluminum increased by about 40%.

In the period 1984–1997, the pH of the low-TOC lakes slightly increased in pH (by ~0.1 unit) (Fig. 2*b*). Only one lake, Övre Skärsjön (topmost line in Fig. 2*b*), showed a greater increase, about 0.4 unit, which was not accompanied by an increase in acid-neutralizing capacity. The pH of two of the high-TOC lakes did not increase in pH, while the other two increased by around 0.3 unit (Fig. 2*d*). As with sulfate, there were larger seasonal variations in pH in the high-TOC lakes compared with the low-TOC lakes. The within-year pH variation (calculated as the mean difference between the highest and lowest pH values during each year for the period 1984–1997) was 0.2–0.5 pH unit for the low-TOC lakes and 0.6–0.9 unit for the high-TOC lakes.

Spheroidal carbonaceous fly-ash particles

All of the studied lakes had very low SCP concentrations at the bottom of the cores and increasing concentrations at depths of 6–15 cm (Fig. 3), presumably due to increased fossil fuel burning after the Second World War. The increasing concentrations of SCP coincided with decreases in diatom-inferred pH, thus correlating the emissions from burning fossil fuels with acidification. Most lakes also showed a clear peak in SCP, interpreted as the 1970 peak, followed by a de-

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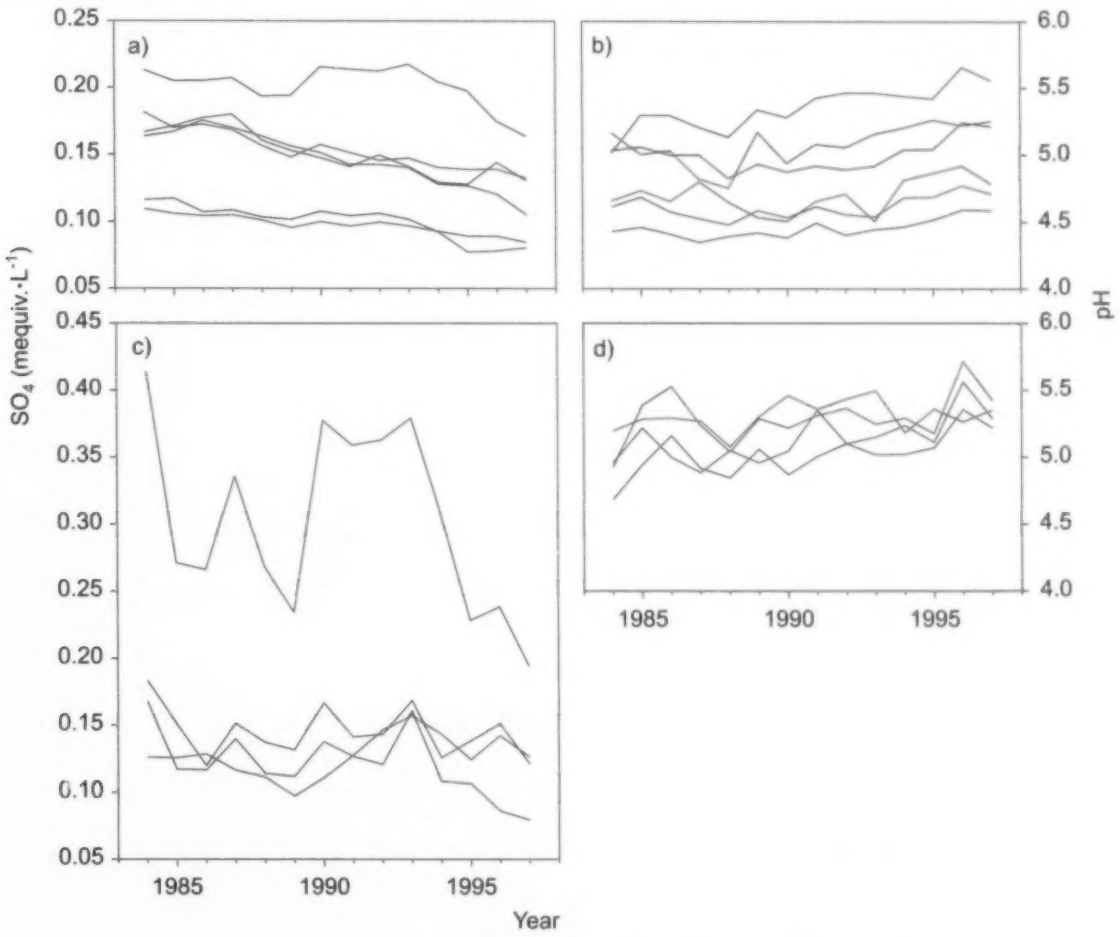
Table 1. Water chemistry data for the studied lakes arranged in order from low- to high-TOC lakes.

Lake	*n*	pH	TOC ($mg \cdot L^{-1}$)	SO_4 ($\mu equiv. \cdot L^{-1}$)	BC ($\mu equiv. \cdot L^{-1}$)	ANC ($\mu equiv. \cdot L^{-1}$)	ΔDpH
Härsvattnet	97	4.5 (±0.01)	2.0 (±0.11)	144 (±2.3)	82 (±2.3)	−106 (±2.6)	−1.1
St. Tresticklan	43	4.6 (±0.02)	3.6 (±0.28)	100 (±2.3)	72 (±2.1)	−60 (±2.7)	−0.8
Örvattnet	48	5.1 (±0.03)	3.8 (±0.17)	97 (±1.2)	104 (±1.8)	−5 (±1.5)	−1.2
Hjärtsjön	52	5.0 (±0.02)	4.0 (±0.36)	201 (±2.6)	199 (±2.9)	−16 (±2.6)	−1.2
L. Öresjön	34	4.7 (±0.03)	5.2 (±0.38)	153 (±3.4)	155 (±4.8)	−36 (±5.3)	−1.3
Ö. Skärsjön	97	5.3 (±0.03)	6.7 (±0.13)	150 (±1.4)	203 (±2.0)	36 (±1.4)	−0.6
Storasjö	85	5.2 (±0.04)	9.4 (±0.31)	122 (±3.1)	173 (±2.5)	44 (±2.5)	−0.6
Rotehogstjärnen	96	5.1 (±0.04)	10.5 (±0.28)	126 (±2.4)	186 (±4.2)	51 (±3.5)	−0.2*
Harasjön	89	5.0 (±0.03)	12.6 (±0.53)	144 (±2.4)	193 (±2.2)	34 (±2.9)	−0.6
Brunnsjön	103	5.3 (±0.02)	17.0 (±0.52)	298 (±7.1)	421 (±6.7)	111 (±3.0)	−0.2*

Note: The water chemistry data are mean values (±1 SE) for the period 1983–1997. Data on acid-neutralizing capacity ($ANC = \Sigma C_B - \Sigma C_A$), base cations (BC), and sulfate (SO_4) are corrected for sea salts. *n* is the number of samples during 1983–1997. The changes in diatom-inferred pH (ΔDpH) refer to the difference between the diatom-inferred pH in the core bottoms (usually >25 cm sediment depth) and that in the core tops (i.e., recent time). An asterisk indicates that the value is within the prediction error of the diatom model (root mean square error of prediction).

Fig. 2. Sulfate concentration and pH (annual means for 1984–1997) in (*a* and *b*) low-TOC lakes (≤6.7 $mg \cdot L^{-1}$) and (*c* and *d*) high-TOC lakes (≥9.4 $mg \cdot L^{-1}$).



crease, reflecting the decreasing emissions since 1970. No clear decrease in SCP was seen in one lake in southwestern Sweden and in the three lakes in southeastern Sweden.

The SCP are derived from both regional and distant sources. The very high concentrations of SCP in some of the lakes reflect the impact of regional sources. The SCP distribution in the 10 lakes analyzed in this study is in general agreement with the distribution found in the surface sedi-

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Fig. 3. Diatom-inferred pH (DpH), SCP concentration, PCs 1 and 2, and a selection of the most common diatom species in the studied lakes. The lakes are arranged in order from low to high TOC concentration. Cyc., *Cyclotella*; Aul., *Aulacoseira*; Tab., *Tabellaria*; Ast., *Asterionella*; Fru., *Frustulia*; Bra., *Brachysira*; Fra., *Fragilaria*; Per., *Peronia*; Eun., *Eunotia*; Ach., *Achnanthes*; Nav., *Navicula*; Cym., *Cymbella*; n.a., not analyzed; d.s., dry sediment.

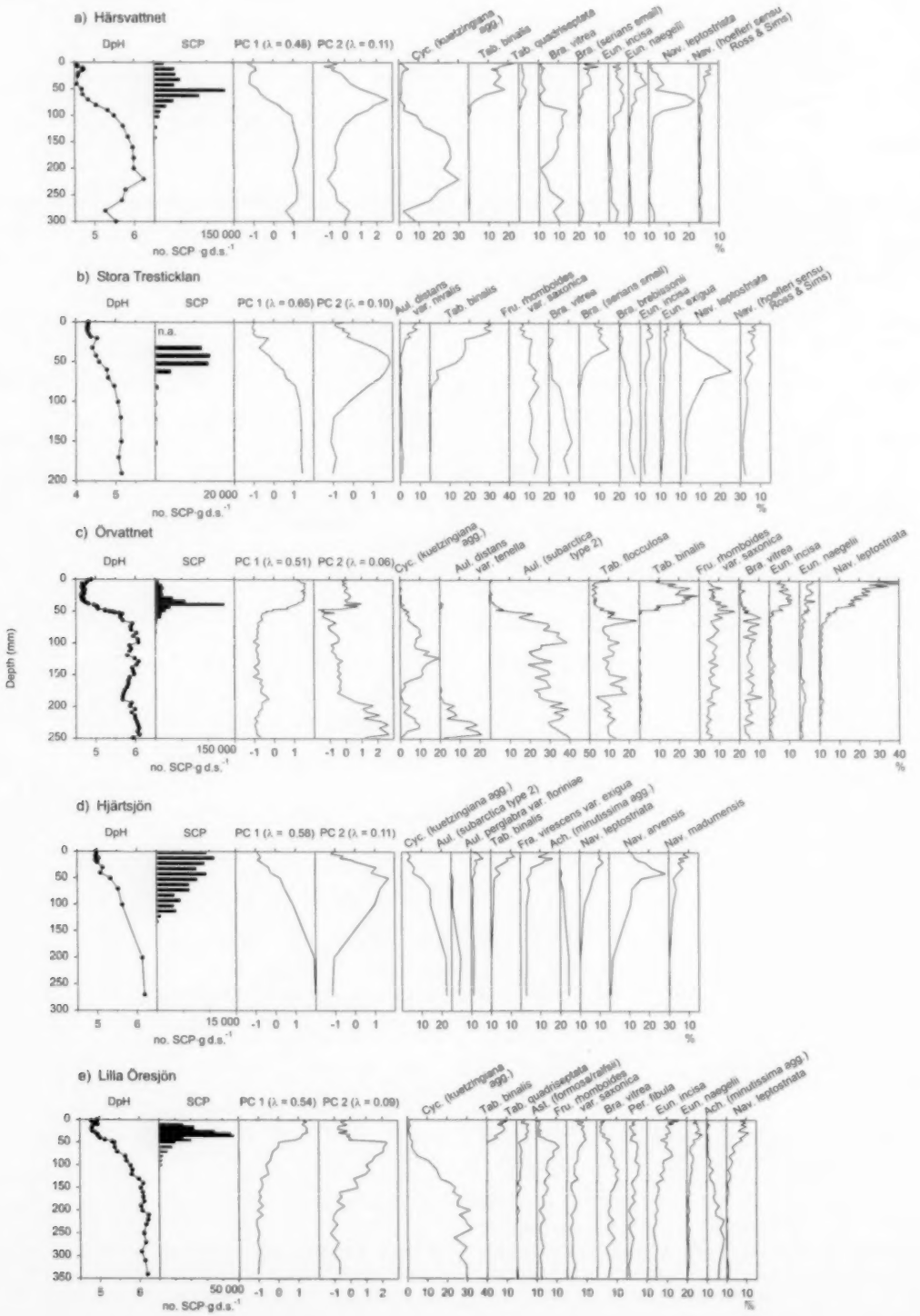

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Fig. 3 (*concluded*).

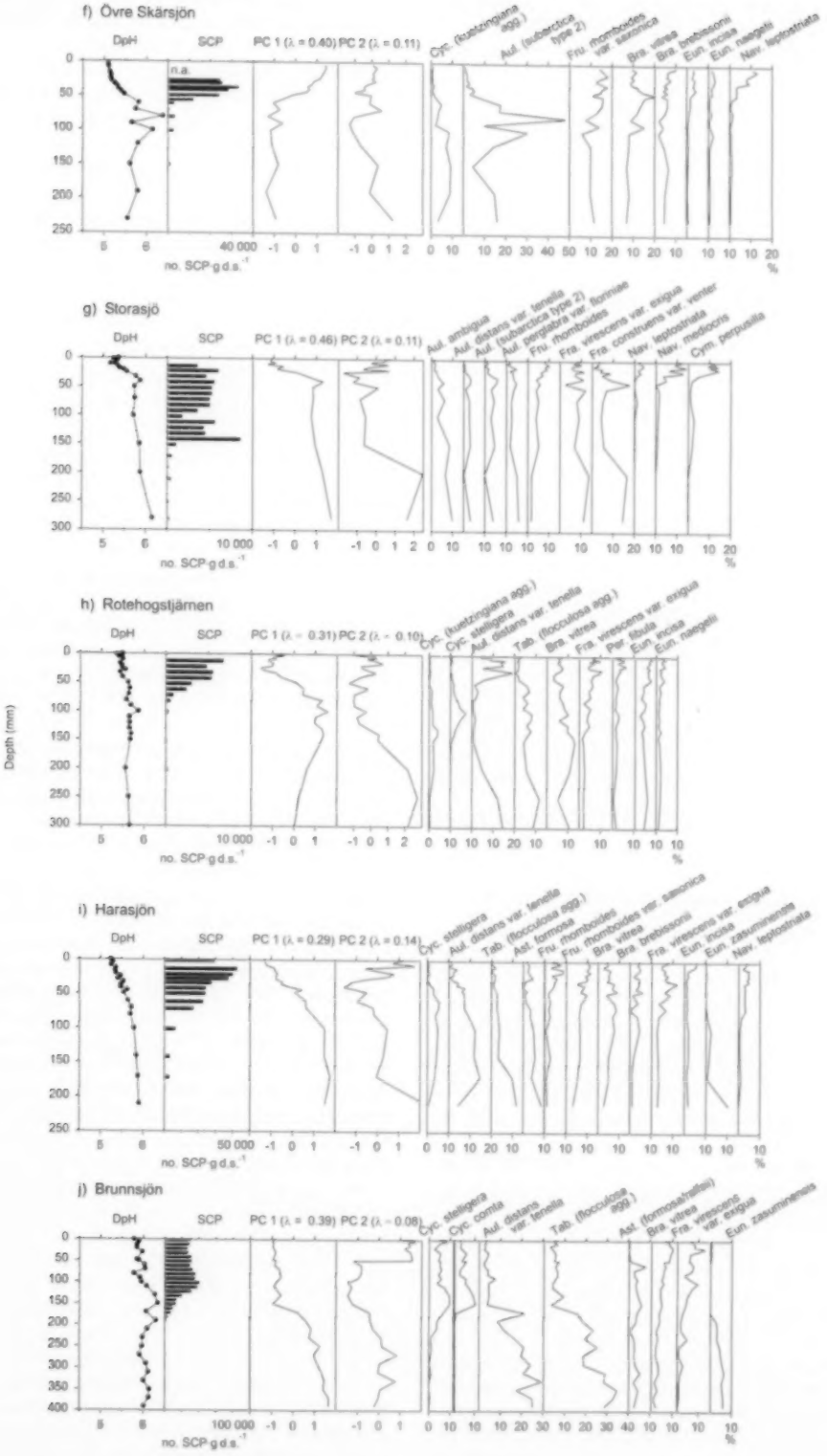

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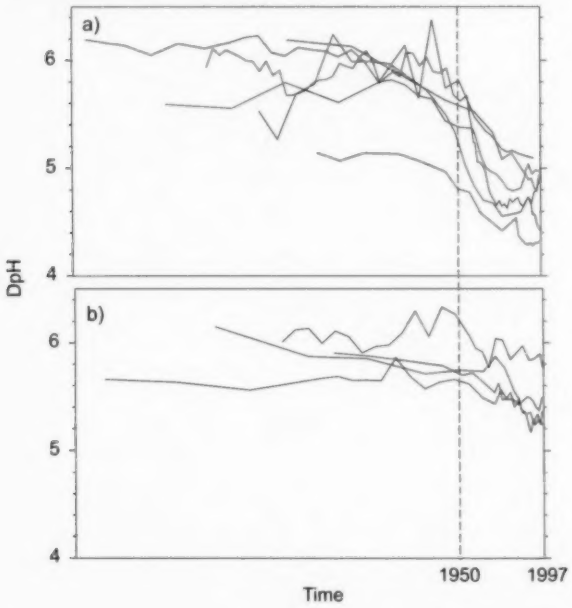
Fig. 4. Diatom-inferred pH of all 10 lakes. (*a*) Low-TOC lakes; (*b*) high-TOC lakes. The different lakes have been correlated in time according to the SCP analysis.



ments of 114 Swedish lakes (Wik and Renberg 1996), with high concentrations in southwestern Sweden and lower levels in the southeastern regions. Storasjö has an unusually extended SCP record that we cannot explain with certainty at present but may be due to early emissions from local glassworks.

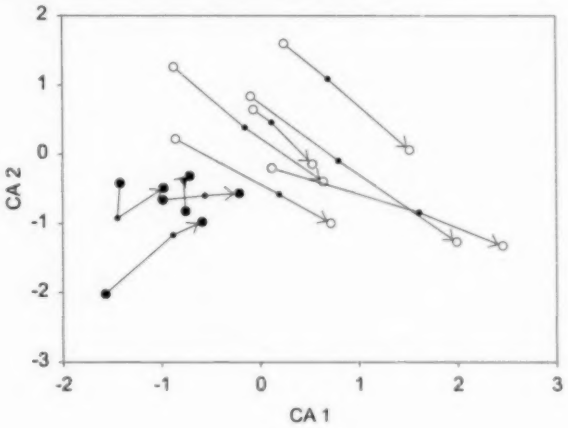
The SCP analyses show that the sediment cores represent at least 150 years. Radiocarbon data obtained in other paleolimnological studies of sediments from Lilla Öresjön and Härsvattnet support these indirect dating results (Renberg et al. 1993).

Diatom-inferred pH trends

Today, all of the lakes are acidic, with pH < 6, according to both the water chemistry measurements and the inferences from the diatom analysis (Table 1; Fig. 3). The diatom-inferred pH values in the surface sediment samples are in good agreement with measured lake water pH. The mean difference between inferred and measured lake water pH for the last 5 years (1993–1997) was 0.23 pH unit; for five of the lakes, the difference was 0.1 pH unit, while the largest difference was +0.5 pH unit (Brunnsjön). Diatom analysis of the sediment cores shows that eight of the lakes are not only acidic but also have acidified in the recent past, diatom-inferred pH decreases varying between 0.6 and 1.3 unit (Table 1). Two lakes, Brunnsjön and Rotehogstjärn, only decreased by 0.2 pH unit, which is within the prediction error of the diatom model (±0.32 pH unit; Stevenson et al. 1991).

Diatom-inferred pH began to decrease before 1950 in many of the lakes, but the major acidification occurred after 1950, according to the indirect dating by the SCP analyses. However, the four high-TOC lakes did not fall to such low pH values as the six low-TOC lakes (Fig. 4). The magnitude of the decrease in pH also differs between the two groups, with the high-TOC lakes decreasing by 0.2–0.6 pH-unit and the low-TOC lakes decreasing by 0.6–1.3 pH unit (Table 1).

Fig. 5. Summary of the CA of diatom assemblages for all 10 lakes. The large markers represent the CA scores for the bottom and surface samples, respectively, while the small markers represent the mean CA score. Solid circles represent high-TOC lakes and open circles represent low-TOC lakes. The direction of change (bottom to surface) is indicated by the arrows.



None of the lakes showed any significant increase in diatom-inferred pH towards the top of the cores. Only in Örvattnet was there a small increase, from pH 4.7 to 4.9.

Multivariate analyses and diatom species trends

The first two axes derived from the CA of the total diatom data set (Fig. 5) clearly differentiate between the six low-TOC lakes (2.0–6.7 $mg \cdot L^{-1}$) and the four high-TOC lakes (9.4–17 $mg \cdot L^{-1}$). Thus, these two groups are characterized not only by contrasting water quality but also by major differences in diatom composition. In the low-TOC lakes, the scores for the first and second CA axes move towards the lower right of the diagram as a result of substantial shifts in the diatom assemblages during acidification. An important part of this shift is the decrease or loss of planktonic species and an increase in benthic acid-tolerant species (Fig. 3). Diatom species with the highest species scores (loadings) for the first CA axis (Fig. 5), which are therefore important for the directed change towards the lower right, include species known to be common in acid lakes, e.g., *Tabellaria binalis*, *Tabellaria quadriseptata*, and acid-tolerant *Eunotia* and *Navicula* species.

To illustrate the changes in the diatom communities in the individual lakes, the scores for the first and second principal components (PCs) of each lake are shown in Fig. 3. The first PC in the acidified lakes is generally related to the species shift resulting in the decrease in diatom-inferred pH and generally has a similar (sometimes mirrored) appearance to the inferred pH curves. This first component explained between 29 and 65% of the diatom variance and reflects species that gradually increase or decrease throughout the core, for example a change from acid-sensitive species to more acid-tolerant species. In the two lakes that have not significantly acidified (Brunnsjön and Rotehogstjärn), the first PC

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reflects variations in factors unrelated to the acidity of the lakes. The second PC, capturing 6–14% of the variance, mainly reflects peaks in single or several species, e.g., *Navicula leptostriata*, which increased in some lakes during early phases of acidification and then decreased as the lake was further acidified.

No recovery could be detected in the analysis of diatom species, except for a small change towards a preacidification flora in Örvattnet. In this lake, the main species change detected was a decrease in *Tabelleria binalis* and *Eunotia incisa* and a corresponding increase in the relative abundance of *Navicula leptostriata*. These changes in the species assemblage are also recorded in the first PC (Fig. 3).

Discussion

In this study, we show that lakes with high and low TOC concentrations have responded differently to similar loads of acid deposition. For instance, Brunnsjön has the highest TOC concentration (17 $mg \cdot L^{-1}$), and it has acidified by only 0.2 pH unit (which is within the error of the model), while Hjärtsjön (4 $mg \cdot L^{-1}$) in the same area has acidified by 1.2 unit. The lakes classified as high-TOC lakes have all acidified to a lesser extent than the six low-TOC lakes.

The contribution of organic acids to lake water acidity has long been recognized (Gorham et al. 1986; Brakke et al. 1987). Paleolimnological analyses of lake sediment cores have demonstrated that many lakes in the acid-sensitive areas of northern Europe (e.g., Renberg et al. 1993) and North America (e.g., Dixit et al. 1992; Cumming et al. 1994) have been naturally acidic for several thousands of years. In acid-sensitive southern Swedish lakes, this natural acidification process has been attributed to leaching of base cations from surface soils and an increase of organic acids from the development of acid podsols and peat (Renberg et al. 1993). This natural acidification process was interrupted ca. 2000 years BP due to land-use changes including burning, forest grazing, and other early agrarian practices that increased the base saturation of the soils. Gorham et al. (1986) and Brakke et al. (1987) found that anthropogenic acid deposition can further reduce the pH in naturally acidic lakes in Canada and southern Norway. However, organic acids not only have the ability to acidify surface waters but also have the capacity to buffer against acidification (e.g., Kortelainen 1993*b*; Hemond 1994), i.e., waters containing organic acids will not acidify to the same extent as waters without organic acids when strong acids are supplied. The acidifying properties are due to the strong organic acids, while the weak organic acids buffer against further decreases in pH if strong mineral acids are supplied. By adding acids, Hruška et al. (1999) demonstrated that the buffering capacity of organic acids was of major significance in a humic stream in northern Sweden.

While organic acids buffer against acidification, they will also be important in buffering against a reversal of acidification, thereby delaying recovery (Hemond 1994; Sullivan et al. 1996). As expected, the six low-TOC lakes show initial reversal of acidification, i.e., gradually decreasing sulfate and base cation concentrations (cf. Skeffington and Brown 1992). In contrast, the four high-TOC lakes have much larger variations of these parameters, suggesting that there are different processes behind the water chemistry trends in these lakes. The amount of peatland in the catchment has been shown to be an important factor for the organic carbon levels in lakes (Kortelainen 1993*a*). Future evaluation of lake chemistry should take into consideration the amount of wetlands in the catchments and the role that reduction and oxidation in these wetlands may play in acidification and recovery (Dillon et al. 1997; Devito et al. 1999).

Despite indications that lake water pH has increased, diatoms do not show recovery, except for a minor recovery in Örvattnet. Since the diatom community in a lake is usually composed of many species with differing pH tolerances, the first sign of recovery is not necessarily an establishment of formerly present acid-sensitive species. Instead the first expected signs of recovery would be shifts in abundance of the species present, as seen in Örvattnet, where *Tabellaria binalis* and *Eunotia incisa* have decreased in abundance, while *Navicula leptostriata* has increased. Since there is no delay due to dispersal of species, diatoms are expected to be sensitive biological indicators of reversing acidification.

It is also possible that the diatom community may have changed in the other lakes, but time lags in the transport of diatoms to the deep basin, together with bioturbation of the surface sediment, may be delaying the detection of such changes (Allott et al. 1992). Örvattnet is the deepest lake in this study and is partly laminated, indicating that its sediments are well stratified. This may partly explain why signs of reversal were first detected in the diatom community of this lake.

Understanding the role of organic acids in association with anthropogenic acid deposition is especially important when assessing the responses to decreasing acid deposition (Driscoll et al. 1994; Hemond 1994; Sullivan et al. 1996). This study has demonstrated how paleolimnological methods can be used to study differences in responses to acid deposition and the that role organic acids may play in this process.

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ERRATUM

Erratum: Effect of spawning day and temperature on salmon emergence: interpretations of a growth model for Methow River chinook

W. Nicholas Beer and James J. Anderson

Ref: Can. J. Fish. Aquat. Sci. **58**: 943–949 (2001).

In Table 1 on page 943, typographical errors occur in the last two rows, i.e., "AM time (month/day)" and "BU time (month/day)." The corrected table appears below.

Table 1. Parameters and results for Methow River chinook salmon egg growth.

Parameter	Downstream, October-spawning, summer-run chinook		Upstream, August-spawning, spring-run chinook
Egg mass, mg	284		218
Day of year of spawning	290		243
Elevation, m	444		560
Range of spawning time, days		15	
Initial embryo mass, mg		1	
Time step (Δt), days		0.25	
AM mass, mg	344		259
BU mass, mg	302		245
AM time, day (month/day)	104 (4/14)		10 (1/10)
BU time, day (month/day)	135 (5/15)		53 (2/22)

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